UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
AGRICULTURAL SCIENCES

Vol. 2, No. 4, pp. 81-190, plates 22-35 November 24, 1919

MUTATION IN *MATTHIOLA*[1]

BY

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CONTENTS

PAGE

Introduction 81
Genetic literature relating to *Matthiola* 84
Methods 85
Experimental data 89
The occurrence of apparent mutants 89
Characteristics and heredity of mutant types 92
1. The early type 92
2. The smooth-leaved type 118
3. The large-leaved type 125
4. The crenate-leaved type 127
5. The slender type 135
6. The narrow-leaved type 141
7. Miscellaneous aberrant types 143
8. Some probabilities of random sampling 145
General discussion 153
Summary 159
Literature cited 161

INTRODUCTION

It is hardly safe to use the term *mutation* without first defining it. In this paper it will be taken to mean a genotypic change, or a change in essential hereditary constitution, due neither to immediate cross fertilization nor to segregation in a heterozygous parent. No attempt will be made to restrict the term to any of the known or supposed types of such genotypic change; a limitation of this kind, which restricts the generally accepted sense of a widely used term, seems to tend to confusion rather than to clearness.

[1] Paper no. 52, University of California Citrus Experiment Station and Graduate School of Tropical Agriculture, Riverside, California.

If we use the term *factor mutation*,[2] (Babcock, 1918) where the cytological change occurs within a locus, transforming a factor into a different factor, two analogous terms will apply where the cytological change is external to the locus. When the cytological change consists of a loss, reduplication, or transposition of one or more loci it may be called a *locus mutation*, and when the change consists in such phenomena affecting a whole chromosome it may be called a *chromosome mutation*. If the term *mutation* is applied to the cytological change itself, the last two types of mutation may be grouped together as extralocus mutations, while the first type consists of intralocus mutations. Examples of factor mutation are white eye in *Drosophila*, and probably the *rubrinervis* type in *Oenothera;* an example of locus mutation is (possibly) "deficiency" in *Drosophila;* and examples of chromosome mutation are *Oenothera gigas* and *O. lata*.

It is now evident that the immediate problem with *Oenothera* relates to the mechanism of heredity in the genus. There are two sharply opposed views. One is that recently emphasized by Atkinson (1917, p. 254), when he says, "The evidence from *Oenothera* cultures points more and more to the conclusion of Shull that 'a hereditary mechanism must exist in *Oenothera* fundamentally different from that which distributes the Mendelian unit-characters.'" The opposing view is represented by Muller's (1918) strictly Mendelian explanation for *Oenothera*, based on "an *Oenothera*-like case in *Drosophila*"; he says, "The striking parallel between the above behavior and that exhibited in *Oenothera* makes it practically certain that this, too, is a complicated case of balanced lethal factors."

A notable feature of the extensive genetic study of *Oenothera* is the lack of progress toward any definitely supported explanation of its hereditary mechanism which is not Mendelian. The only definite non-Mendelian hypothesis of chromosome behavior so far proposed, aside from "merogony" and other hypotheses (Goldschmidt, 1916) apparently possible but not proved for *Oenothera*, which assume loss of chromatin after fertilization, seems to be Swingle's (1911) "zygotaxis," proposed for the apparently parallel case of *Citrus*. This suggestion that F_1 hybrids may differ, apart from non-uniformity of the P_1 gametes, because of the establishment of permanently different arrangements of the chromosomes in the fertilized egg, still seems to be purely speculative.

With more or less "*Oenothera*-like" cases in other genera, the only definite progress in analysis seems to have resulted from the assump-

[2] Muller (1918) has recently used *point mutation* in the same sense.

tion of Mendelian segregation. With *Oenothera* itself, the trend of the evidence tends to favor this form of explanation.

This fact is strikingly illustrated by two papers of de Vries (1918, 1919) which have appeared since the present paper was written, especially as Muller's (1918) complete report on the beaded-wing case in *Drosophila* (see especially pp. 471–474, 489, and 498–499) indicates that de Vries had hardly yet realized the full possibilities of the balanced-factor hypothesis. In the light of Muller's masterly demonstration of these possibilities, we may be confident that "mass mutation" is merely ordinary segregation, and that the "unisexual" crosses of *Oenothera* are really "Mendelian" in their essential phenomena. Some difference of usage respecting the inclusiveness of the term *Mendelian* may be involved here, it is true, since apparently de Vries would apply it only to cases where strictly homologous factors are opposed in homologous chromosomes. Since, however (Muller, 1918), there are good reasons for expecting the occurrence of gradations of similarity and of synaptic attraction between opposed loci, and hence of gradations of linkage, the criterion of Mendelian behavior should obviously be the occurrence of segregation between homologous chromosomes, whatever their degree of similarity or amount of crossing over. We have no reason to assume that an "unpaired" factor in a parent would so divide as to be included *in all gametes;* on the other hand, we have learned of a mechanism capable of insuring, in certain particular cases, the inclusion of a certain factor or group of factors either in every *functional* gamete or in every *viable* zygote.

No doubt, as Davis (1917) says, "A great forward step will be taken in *Oenothera* genetics when types of proven purity have been established . . . ." Meanwhile, cases of "*Oenothera*-like" heredity in species known to possess the Mendelian mechanism deserve most thorough investigation. Special interest consequently attaches to the peculiar inheritance of certain apparent mutations of the ten-weeks stock (*Matthiola annua* Sweet), a species in which various characteristics are typically Mendelian. A remarkable series of aberrant forms in this species[3] has been briefly discussed in two preliminary communications (Frost, 1912 and 1916), and the present paper gives a fuller account of the same phenomena.[4]

[3] In the variety "Snowflake," a glabrous, double-producing form with white flowers.

[4] While this paper was in press Blakeslee and Avery (1919), have reported the occurrence of apparent mutations in *Datura,* which seem to be similar in almost every respect to those here discussed.

Apparent mutants were first found in the course of work on another problem, the relation of temperature to variation (Frost, 1911), conducted at Cornell University. Studied incidentally at first, these new forms were later given special attention. About nine thousand plants, of which about two thousand were progeny of mutant-type parents of peculiar heredity (nearly one-fourth of the latter representing crosses with Snowflake), have been examined altogether. Some of these plants have been grown at Riverside, where hybridization studies with mutant types are in progress. The present account considers the origin and characteristics of these types, their inheritance with self pollination, and the rather meager available data relating to their behavior in crossing.

In connection with the work at Cornell, special acknowledgment is due to the late Professor John Craig, and to Dr. H. J. Webber and Dr. H. H. Love. Facilities for work were furnished by the departments of Horticulture and Plant Breeding of the New York State College of Agriculture.

GENETIC LITERATURE RELATING TO *MATTHIOLA*

The work of Correns (1900) on *Matthiola* furnished one of the earliest confirmations of Mendel's law, and also pointed to complications not found by Mendel. The earlier literature, according to Correns, gives no indication of the study of *Matthiola* hybrids beyond the first generation.

In his later paper on aberrant hybrid ratios, the same author (1902) discusses complications in maize and in *Matthiola*. After referring the deviations found in maize to selective pollination, he considers a suggestion of de Vries relating to environmental modification of Mendelian ratios, and himself suggests the possibility of selective elimination of gametes. He says (pp. 171–172), "Solche Einflüsse brauchten nicht alle Sorten Keimzellen des Bastardes gleichmässig zu treffen, sondern sie könnten eine Sorte stärker angreifen als die andere."

Von Tschermak (1904, 1912) has made extensive studies of *Matthiola* hybrids, considering mainly, as did Correns, pubescence and flower color. The latter of these papers on hybrids in the genera *Matthiola, Pisum,* and *Phaseolus* represents a careful analytical test of the "factor hypothesis" of segregating inheritance, leading to the conclusion that the applicability of this hypothesis is strongly con-

firmed by the results secured. This work, with that of Miss Saunders, leaves no possibility of doubt that the typical Mendelian mechanism is present in *Matthiola*.

The most extensive genetic work on *Matthiola* is evidently that of Miss Saunders, reported by herself (1911, 1911*a*, 1913, 1913*a*, 1915, 1916) and by Bateson and Saunders, with others (1902, 1905, 1906, 1908). This also is work on heredity in hybrids, with special emphasis on the factorial interpretation of the various complications relating to pubescence and to "doubleness" of flowers.

Goldschmidt (1913) has explained the inheritance of doubleness by sex linkage and lethal action of a femaleness factor in pollen formation, and his interpretation has been criticized by Miss Saunders (1913). I (Frost, 1915) have presented a somewhat different lethal-factor scheme, and Miss Saunders (1916) has since restated her views and criticized mine.

Muller (1917) has cited the inheritance of doubleness as a case of "balanced factors," in apparent agreement with my formulation.

Apparently no one but the present writer (Frost, 1912, 1916; see also review by Bartlett, 1917) has reported experimental evidence of any notable tendency to apparent mutation in the genus, although de Vries (1906, p. 338) mentions the occasional occurrence of vigorous, rigidly upright individuals (a *gigas* type?), known at Erfurt as "generals," and refers to the rare mutative occurrence of single flowers on branches of double-flowering plants. Doubleness, and color variations in considerable number, have evidently arisen under cultivation, probably through mutative changes.

METHODS

The general cultural methods employed for the first three generations have been very briefly described elsewhere (Frost, 1911).

The plants of the first four years were grown in pots in the greenhouse. The plants of the first generation came from one or both of two packets of commercial seed planted in the fall of 1906, and all plants in the later cultures (possibly excepting series 18) were descendants of these. The cultures will in general be designated by the year in which the seed was sown; the field and greenhouse cultures of 1911 are indicated by 1911F and 1911H respectively.

Part of the seed planted, especially in 1908, came from unguarded flowers. The seed lots where this occurred will be indicated in the

tabulation of parental data by italic figures, while protection possibly defective will be indicated by an asterisk. It is not probable that much viviism occurred in the greenhouse cultures, since this plant is well adapted to self fertilization.

In the first year's (1906) cultures the plants in each experimental environment were separately numbered. Each plant was designated by its number preceded by two letters indicative of the environment. For greenhouse temperature these letters were C (cool), M (medium temperature), and W (warm); for potting soil[5] they were S (sand), L (unfertilized "loam"), and G ("good" soil, fertilized). Thus CS1 CS2, WG9, etc., were pedigree numbers of the first generation, and CG2–M8 and WG9–C10 of the second generation. A few syncotyledonous plants outside the regular cultures of 1907 were called WG9–syn1, etc.

For the work at Riverside a new system of numbering was adopted, better suited to ordinary pedigree cultures, and the numbers from this system are used below in the individual treatment of all but one of the mutant types ("early"). This is essentially Webber's (1906, p. 308) system, except that each initial or P_1 individual of a series is indicated by a letter; a full description has been published (Frost, 1917). With *Matthiola* each type or cross between two types that is tested receives a series number, the apparent mutants themselves always being taken as the initial individuals of their selfed series.

The cultures of 1908 included progeny of various parents, one being WG9–C10, an early and few-noded plant suspected of being a mutant.

The cultures of 1910 consisted of a second-generation test of WG9–C10, and a first-generation test of other possible mutants, with control lots. The plants were all grown on one bench in one greenhouse (house C), from thirty lots of fifteen seeds each, lots 1–17 relating to WG9–C10. The parents descended from WG9–C10 (see table 7) were selected as those with fewest internodes, a medium number of internodes, and most[6] internodes in each house of the 1908 cultures, earliness of flowering being considered when parents were alike in number of internodes. The control parents were both few-noded and many-noded, relatively to their sibs.

In 1911 eighty progeny lots were grown in the field at Ithaca. Lots 1 to 28, transplanted from the greenhouse, paralleled the test of

[5] Soil experimentally varied only in the 1906 cultures, temperature varied in the two following years also.

[6] For house M, not the highest, which was exceptionally high, but the next to the highest.

WG9–C10 made in 1910–11; all available progeny of WG9–C10, except the crenate-leaved apparent mutant WG9–C10–C10, were tested, with check lots between as before. Soil differences and unavoidable differences between lots in time of transplanting combined with hot weather and drought to reduce the value of the results. The remaining fifty-two lots, all field-sown, included a further test of the heredity of aberrant types other than early. Most of these lots, however, were progeny of Snowflake parents, grown to obtain evidence on the relation of temperature to mutation and on the inheritance of doubleness of flowers, and therefore the results are not reported here.

The 1911II cultures constituted a coldframe and greenhouse progeny test of mutant types, mainly in the second generation, the plants being grown in flats.

There was added in 1912–13 a small greenhouse test bearing on the supposed mutative origin of WG9–C10, in view of the apparent possibility that WS1 or WL10, in the same house with the unbagged WG9, might have been heterozygous for the early type—cross pollination then giving the apparent mutant.

Further progeny tests of the mutant types have been made in the field at Riverside, beginning in the fall of 1913. Mainly on account of the unsuitability of the usually hot and dry climate of Riverside, the cultures have been largely experimental and always on a small scale, and germination or development has sometimes been unsatisfactory. Cultures have been started in October, November, January, and February, and a trial culture in progress at the time of writing was started in August. Some of the plants of the 1915–16 cultures were kept until the summer of 1917, and many of them flowered for the first time when about a year old.

In the cultures of 1913, growth was largely unsatisfactory, and with part of the plants aphid injury interfered more or less with the classification of types. In the cultures of 1914, the seeds were largely lost through toxic effects favored by very shallow planting (as at Ithaca) and strong evaporation from the soil. In subsequent planting, the seeds, planted singly in small paper pots, were dropped into relatively deep holes punched in the soil, and covered with sand.

The only field-grown plants closely resembling those grown in the greenhouse at Ithaca, it may be noted, have been those of the 1917 cultures, grown in a lathhouse with added shade from muslin.

In the cultures of 1915–16, with partial shade and more frequent irrigation than before, development was in general good; but even

TABLE 1

Cultures of 1908. Aberrant types: occurrence among progeny of Snowflake parents.

Parentage	Progeny											
			Numbers evidently belonging to aberrant types									
	Selection	Total number	Smooth-leaved type	Crenate-leaved type	Semi-crenate-leaved type[d]	Narrow-leaved type	Slender type	Leaf-tips misshapen; very late	Leaves numerous and small; very late	Petals spatulate; very late	All apparent mutants	
											Number	Per cent
CG2	None	85	3	1	.....	.....	.....	.....	.....	.....	4	.....
WS1	None	38	.....	1	1	.....	1	.....	.....	.....	3	.....
WL10	None	34	.....	1	.....	1	.....	1	1	.....	4	.....
WG9	None	117	2	.....	.....	1	.....	.....	.....	1	4	.....
All above	None	274	5[b]	3	1	2	1	1	1	.....	15	5.47 ± .93[e]
All above	Selection in notebook[a]	208	1	1	.....	.....	.....	.....	.....	.....	2	.96 ± 1.06
CG2–F_1 and WG9–F_1	Selection at transplanting	440	1	2[c]	.....	.....	1	.....	.....	.....	4	.91 ± .73

[a] By including all potted plants in each arranged progeny lot (see "Methods," p. 89) up to the first that probably would have been rejected from a selected lot at transplanting.

[b] Another, a tricotyledonous seedling of CG2, occurred among unpotted plants.

[c] Two others occurred among 11 syncotyls potted ("extra" plants); parents, CG2–W1 and CG2–W9.

[d] Another among unpotted plants (parent, WG9–W2).

[e] The percentage for this unselected lot is used as p for all three probable errors. See p. 145 for the general method of calculation, etc.

here the mutant types, with one exception, often failed to grow satisfactorily or to set seed. Infection, probably by *Fusarium*, evidently was the cause of the death of many of these plants in their second season.

With all cultures grown after (probably) those of 1906, special care was taken to secure random samples of seed, and after 1908 no plants were rejected. The only exception to this statement is the rejection of one pot out of every fifteen, by number and systematically, in the first twenty progeny lots of 1910. For the earlier cultures, a certain amount of selection must be recorded, as follows. In 1906 the small and the largest plants were omitted at potting, and probably any weak and abnormal seedlings had been omitted at the preceding transplanting. In 1907 all markedly weak, late, or abnormal seedlings, as determined mainly by the appearance of the cotyledons, were omitted at the first transplanting; and the same was done in 1908, except that certain lots from old seed were unselected.[7]

These last lots were arranged at transplanting in such a way that the weak and abnormal plants came at the end in each lot.

EXPERIMENTAL DATA

The Occurrence of Apparent Mutants

In the cultures of 1906, 88 plants were grown to maturity, none of these being suspected of mutation. In the cultures of 1907, among 170 plants one striking variant appeared; this plant, WG9–C10, was exceptionally small and early in blooming.

In the cultures of 1908, 714 plants were available, including apparent mutants in several hereditary lines as indicated in table 1. A striking feature of the results is the scarcity of apparent mutants among the seedlings classed as strictly normal at transplanting; probably the scarcity in the preceding years was due mainly to the rejection of abnormal seedlings (see "Methods"). The first, second, and fourth of these forms have been common in later cultures, while the third and fifth have been rarer; the last three, if seen at all elsewhere, have not being recognized as belonging to the same types as these three plants.

[7] One tiny plant from WG9, probably not viable, was discarded.

Table 2 shows the numbers and percentages of apparent mutants found in the cultures of 1910 and 1911F. Since the early type seems to differ from Snowflake only in size and earliness, and is probably inherited without special complications, the available progeny of early-type parents are included in the totals. The progeny of all parents recognized as belonging to other aberrant types are omitted. The second column under "Percentage of mutants" omits doubtful types and individuals, but includes some individuals for which some doubt was indicated in the original records. One rare type of 1911, large-

TABLE 2

Aberrant types: occurrence among progeny of Snowflake and early parents. Apparent selective elimination at or after germination in field-sown cultures.[a]

Cultures	Progeny examined[b]	Percentage of apparent mutants	
		All counted	Doubtful omitted
Greenhouse, 1910	338	5.03 ± .82[c]	4.14 ± .77
Field, 1911, seed house-sown	2072	5.31 ± .33	4.63 ± .31
All above	2410	5.27 ± .31	4.56 ± .29
Same, Snowflake parents only	1364	4.33 ± .41	3.74 ± .38
Field, 1911, seed field-sown (parents all Snowflake)	3927	2.34 ± .24	1.55 ± .22

[a] Germination in greenhouse-sown lots, counting only plants examined for type, 93.2 per cent; in field-sown lots, 45.1 per cent.

[b] Including some plants of uncertain type, indicated for some lots (when apparently not Snowflake) in tables 1 and 3.

[c] For the calculation of these probable errors the percentages on the third line are used as p.

leaved, here omitted, has proved to be genetic, but its determination in these cultures was in general uncertain. A stricter criterion for the second column, elimination of all individuals not considered positively determined, was used in the calculations for the tables for the inheritance of the separate mutant types.

Evidently the more rigorous field conditions of 1911 eliminated many of the "mutants" at or soon after germination. The "coefficient of mutability" with good germination, as was the case with the unselected cultures of 1908, seems to be near 5 per cent, a surprisingly high figure if immediate true mutation is responsible.

Before the aberrant types are considered separately, we may examine (table 3) a detailed illustration of their occurrence in larger cultures. It seems probable, from this evidence, that any descendant of WG9 was capable of producing any of the mutant types so far

TABLE 3

1911, field; plants transplanted from greenhouse. Aberrant types: occurrence among progeny of Snowflake and early parents.[a]

Field lot	Ancestry: Generation 1	Ancestry: Generation 2	Ancestry: Generation 3	Total progeny of determinable type	Progeny evidently belonging to aberrant types: Smooth-leaved	Small-smooth-leaved	Crenate-leaved	Semi-crenate-leaved	Pointed-crenate-leaved	Medium-smooth-leaved	Narrow-leaved	Narrow-dark-leaved	Slender	Small-convex-leaved	Compact	Curly-leaved	Pointed-light-leaved	Large-leaved	Medium-large-leaved	Large-thick-leaved	Small stout-capsuled	Jagged-leaved	All types: All counted	All types: Doubtful omitted
1	WG9	C5	C8	77	1							2											3	3
2			C10	70	1														1 (?)				2	1
7			W18	77	1			1			1	1								1 (?)			5	4
8			W24	75	1		1					3											5	5
15		C9	C3	78											2								2	2
16			C7	75	1		1				1												3	3
27			W10	73		1	1			1	1												4	4
28			W24	78	1	1		1															3	3
26				59	3			1			1												5	5
3		C10	C2	79	3	1	1					1		1							1 (?)		8	7
4			C5	78	2		1				1	1										1 (?)	6	5
5			C8	78							1												1	1
6			C1	76							2												2	2
9			M4	76	2		1		1														4	4
10			M9	78		1					1								1 (?)				3	2
11			M6	77	1	1	2																4	4
12			M2	77	2	1											1 (?)						4	3
13			M7	80	2						1					1		1 (?)	1 (?)				6	4
14			M8	70							2												2	2
17			W6	70	1		1				1	2	1 (?)										6	5
18			W4	65	1	1	1						1 (?)				1 (?)						5	3
19			W11	76																			0	0
20			W9	72		1									1								2	2
21			W5	75	1			1			2				1								5	5
22			W8	74	2	1					5												8	8
23			W7	72	1		2										1 (?)						4	3
24			W3	71																			0	0
25			W10	66			4						1	1						2 (?)			8	6
All parents—totals				2072	27	9	16	4	1	1	20	10	3	2	4	1	3	1	3	3	1	1	110	96
All parents—percentages				100	1.30	.43	.77	.19	.05	.05	.97	.48	.14	.10	.19	.05	.14	.05	.14	.14	.05	.05	5.31	4.63

[a] Individuals with "?" are those considered to be possibly Snowflake. A few others are somewhat uncertain as to type, though evidently not Snowflake. Possibly some of the rarest types should be merged with others. One plant in lot 28, observed before the first regular examination for type as apparently dead and of crenate-leaved type, was omitted.

discovered; the occurrence of the various types suggests a random distribution among the progeny lots. This conclusion is confirmed, and extended to CG2, by the field-sown lots of 1911.

Various parents belonging to mutant types have given other mutant types among their progeny. There is some reason, as table 4 indicates, to suppose that parents of the early type have a more marked tendency to produce these other types than have Snowflake parents.[8]

TABLE 4

1910 and 1911F; sown in greenhouse. Apparent mutants among descendants of WG9–C10 and other ancestors, comparing early parents (pure or hetcrozygous) with Snowflake parents.

Ancestry	Type of parent	Progeny		
		Total examined	Percentage of mutants	
			All counted	Doubtful omitted
WG9–C10	Early	1046	6.50 ± .47[a]	5.64 ± .44
	Snowflake	558	4.30 ± .64	3.41 ± .60
Pure Snowflake	Snowflake	806	4.34 ± .53	3.97 ± .50
Both	Snowflake	1364	4.33 ± .41	3.74 ± .38
Both	Both	2410	5.27 ± .31	4.56 ± .29

[a] For the calculation of these probable errors the percentages on the last line are used as *p*.

Characteristics and Heredity of Mutant Types

1. THE EARLY TYPE

So far as is known, WG9–C10 (figs. 1, 2) was the only apparent mutant of the early type in the cultures. Since, however, this type visibly differs from Snowflake only or mainly in quantitative characters, it cannot be positively identified without comparative progeny tests, and therefore may have been represented by mutant individuals not used as parents. WG9–C10 was much smaller proportionately than were its progeny; this difference was probably due to an embryonic abnormality, early blind termination of the main axis, which was occasionally observed elsewhere and probably occurred in this case. Plants of this type, as compared with Snowflake, are, in general, fewer-noded, smaller, and earlier in blooming.

The principal data from the cultures of 1908 are shown in tables 5 and 6, which also indicate the later conclusions as to the segregation of the early type in the cultures of this year; figures 3 and 4 illustrate

[8] Inspection of the data in detail indicates that this difference is not due to the possible tendency in parents grown in the warm house to more frequent apparent mutation.

TABLE 5

Cultures of 1908. Time from sowing to emergence of corolla of earliest flower of primary cluster. Frequency distributions.[a]

Parents:	Singles						Doubles					
	House C		House M		House W		House C		House M		House W	
	WG9–C10	Rest	WG9–C10	Rest	WG9–C10	Rest	WG9–C10	Rest	WG9–C10	Rest	WG9–C10	Rest
Days [b]												
110	....	....	1‡	....	....	....	....	....	....	....	....	....
111	....	....	1‡	....	....	....	....	....	....	....	....	....
112	....	....	....	....	....	....	....	....	....	....	....	....
113	....	....	....	....	....	....	....	....	....	....	....	....
114	....	....	....	....	....	....	....	....	....	....	....	....
115	....	....	....	....	....	....	....	....	....	....	....	....
116	....	....	....	1	....	....	....	....	1	....	....	....
117	....	....	....	....	1‡	....	....	....	....	....	....	....
118	....	....	1‡	2	....	....	....	....	....	....	....	....
119	....	....	....	3	....	....	....	....	....	....	....	....
120	1‡	....	....	4	....	....	....	....	....	....	....	....
121	....	....	1‡	2	....	....	....	....	....	1	....	1
122	....	....	....	3	....	....	....	....	....	....	....	2
123	....	....	....	8	1‡	....	....	....	1	1	....	2
124	....	....	1	4	....	....	....	....	....	1	....	2
125	....	....	....	7	1‡	....	....	....	....	5	1	3
126	....	....	....	16	....	....	....	....	....	7	....	7
127	....	....	....	3	1‡	2	....	....	....	9	....	2
128	....	....	....	4	....	3†	....	....	....	8	....	5
129	....	....	....	7	1‡	4	....	....	....	8	....	7
130	....	....	....	1	1‡	3	....	....	....	12†	....	4
131	....	1	....	2	....	4	....	....	2	12	....	3
132	1‡	....	....	1	....	2	....	....	....	7	....	8
133	1†‡	....	....	1	1	....	....	....	....	4	....	7
134	1	2	....	2	....	1	....	....	....	2	....	7
135	....	4	....	4	....	4	....	....	....	6	....	6
136	....	1	1	1	....	3	1	....	....	....	....	4
137	....	7	....	2	....	3	....	3	....	1	....	2
138	....	10	....	1	....	9	....	4	....	1	....	1
139	....	18†	....	1	1	2	....	8	....	1	....	3
140	1	7	....	1†	....	4	....	13	....	....	....	3
141	....	10	....	....	....	1	1	9	....	1	....	3
142	....	4	....	....	....	6	....	15	....	1	....	1
143	....	4	....	....	1	5	2	10	....	....	....	2
144	....	4	....	....	....	2	....	9	....	....	....	2
145	....	....	....	....	....	3	....	6	....	....	....	3
146	....	....	....	....	....	....	1	5	....	....	....	2
147	....	....	....	....	....	....	....	4	....	....	....	....
148	....	....	....	....	....	2	....	1	....	....	....	1
149	....	....	....	....	....	2	....	1	....	....	....	....
150	....	1	....	....	....	1	....	2	....	....	....	....
151	....	1	....	....	....	....	....	1	....	....	....	1
152	....	....	....	....	....	....	....	....	....	....	....	2
153	....	1	....	....	....	....	....	....	....	....	....	1
154	....	....	....	....	....	....	....	....	....	....	....	....
155	....	1	....	....	....	....	....	1	....	....	....	1

[a] Daggers (†) indicate the position and number of apparent mutants. Double daggers (‡) indicate inheritance of parental type (here, early); all *single* progeny of WG9–C10 here reported have been tested for inheritance of this type. The conventional statistical constants corresponding to the house totals of tables 5 and 6 have been published (Frost, 1911); the means for flowering given there are too high by one half-day.

[b] To time of observation (upper limit of one-day class).

TABLE 5. CULTURES OF 1908 (*Continued*)

Parents:	Singles						Doubles					
	House C		House M		House W		House C		House M		House W	
	WG9–C10	Rest	WG9–C10	Rest	WG9–C10	Rest	WG9–C10	Rest	WG9–C10	Rest	WG9–C10	Rest
Days [b]												
156	....	....	....	....	....	....	....	....	....	....	....	....
157	....	....	....	....	....	....	....	....	....	....	....	....
158	....	....	....	....	....	....	....	....	....	....	....	....
159	....	....	....	....	....	....	....	....	....	....	....	....
160	....	....	....	....	....	....	....	....	....	....	....	....
161	....	....	....	....	....	....	....	....	....	....	....	1
162	....	....	....	....	....	....	....	....	....	....	....	....
163	....	....	....	....	....	....	....	....	....	....	....	....
164	....	....	....	....	....	....	....	....	....	....	....	....
165	....	....	....	....	....	....	....	....	....	....	....	....
166	....	....	....	....	....	....	....	....	....	....	....	....
167	....	....	....	....	....	....	....	....	....	....	....	1†
168	....	....	....	....	....	....	....	....	....	....	....	....
169	....	....	....	....	....	....	....	....	....	....	....	....
170	....	....	....	....	....	....	....	....	....	....	....	....
171	....	..	....	....	....	....	....	....	....	....	....	....
172	....	....	....	....	....	....	....	....	....	....	....	....
173	....	1†	....	....	....	....	....	....	....	....	....	....

[a] Daggers (†) indicate the position and number of apparent mutants. Double daggers (‡) indicate inheritance of parental type (here, early); all *single* progeny of WG9–C10 here reported have been tested for inheritance of this type. The conventional statistical constants corresponding to the house totals of tables 5 and 6 have been published (Frost, 1911); the means for flowering given there are too high by one half-day.

[b] To time of observation (upper limit of one-day class).

the difference in earliness between the early and Snowflake types. The parents grouped under "rest" include CG2 and WG9 themselves, with four progeny of the former and eight of the latter. Of these fourteen parents, not one has produeed exceptionally few-noded progeny like those of WG9–C10.

Apparently WG9–C10 was heterozygous for a "few-nodedness" faetor not carried by any of the other parents tested. Neither in the 1907 cultures nor in the 1908 cultures now under eonsideration did the data suggest that WG9 itself was similarly heterozygous. Tables 5 and 6 inelude the first 30 progeny of WG9, for each house, as arranged at the first transplanting,[9] 88 plants altogether; ineluding the remaining plants, mainly weak or abnormal at transplanting, the total is 116. One of the F_2 plants (WG9–syn 3–M10) was very suggestive of the early type, but (tables 12 and 13) it gave only Snowflake progeny in a small test.

[9] See page 89. Two plants not producing a normal main inflorescence are omitted.

TABLE 6

Cultures of 1908. Number of main-stem internodes below first flower-bearing node. Frequency distributions.[a]

	Singles						Doubles					
	House C		House M		House W		House C		House M		House W	
Parents:	WG9–C10	Rest	WG9–C10	Rest	WG9–C10	Rest	WG9–C10	Rest	WG9–C10	Rest	WG9–C10	Rest
Internodes												
16	1‡	..	..	....	..	..	....	....	....	....	....	....
17	....	....	..	....	....	....	....	....	....	....	....	....
18	....	....	....	....	..	....	..	....	....	....	..	....
19	1‡†	....	..	..	....	..	....	....	....	....	....	....
20	1‡	....	..	..	..	..	1	....	....	....	....	....
21	....	..	2‡‡	....	..	....	..	....	....	....	....	....
22	....	..	1‡	....	..	....	1	....	1	....	....	....
23	..	..	..	....	....	....	....	....	1	....	....	....
24	..	..	..	....	....	..	..	9	....	....	....	....
25	1	2†	1‡	1	..	..	2	25	..	....	....	....
26	..	..	..	....	....	..	..	29	....	1	....	....
27	1	7	..	1	..	..	1	22	....	2†	....	....
28	..	17	..	....	....	..	..	6	....	9	1	....
29	..	24	..	1	..	..	..	....	....	14	..	....
30	..	13	..	1	....	..	....	1	2	22	....	1
31	....	8	..	2	....	..	..	..	..	27	..	..
32	..	2	..	7	..	..	..	..	..	5	..	..
33	..	1	..	15	1‡	..	..	..	..	3	..	..
34	..	..	1	16	....	....	..	....	..	4	..	1
35	..	2	..	19	1‡	....	..	....	..	..	..	5
36	....	....	..	4	1‡	....	..	....	....	1	..	6
37	....	....	..	1	1‡	....	....	....	....	..	..	8
38	....	..	..	8	..	....	....	....	....	....	..	5
39	....	....	..	3	..	....	....	....	....	....	..	13
40	..	..	..	1	..	....	....	....	....	....	....	6
41	....	..	1	1†	..	....	....	....	....	....	....	8
42	....	1†	..	....	1‡	..	....	....	....	....	....	6
43	....	....	..	....	..	1†	....	....	....	....	....	12
44	....	....	..	....	..	....	....	....	....	....	....	9
45	....	....	....	....	1‡	....	....	....	....	....	....	6
46	....	....	....	....	....	4	....	....	....	....	..	3
47	....	....	....	....	....	3	....	....	....	....	....	3
48	....	....	....	....	..	4	....	....	....	....	....	....
49	....	....	..	....	1	3	....	....	....	....	....	1
50	....	....	..	..	..	6	....	....	....	....	....	....
51	....	..	....	....	1	3	....	....	....	....	....	2†
52	....	..	....	....	....	10	....	....	....	....	....	1
53	....	..	..	....	....	6	....	....	....	....	....	....
54	....	..	..	....	..	2	....	....	....	....	....	2
55	....	....	....	....	1	3	....	....	....	....	....	....
56	....	..	..	..	..	7	....	....	....	....	....	1
57	....	..	..	..	..	8	....	....	....	....	....	....
58	....	....	..	..	....	1	....	....	....	....	....	....
59	....	....	..	..	....	1	....	....	....	....	....	1
60	....	....	..	..	....	3	....	....	....	....	....	..
61	....	..	..	..	....	..	....	....	....	....	....	..
62	....	....	..	..	..	1	....	....	....	....	....	....

[a] See note *a* to table 5.

The differentiation of the early race is very marked; with the singles, in fact, the later cultures indicate no ease of overlapping in the 1908 cultures, in either character, between extracted pure Snowflake and pure or heterozygous early. The total sterility of the doubles necessarily leaves their constitution somewhat in doubt.

The cultures of 1908 so far suggest that WG9–C10 was a mutant. To be reasonably certain, however, we must have further evidence (1) on the fact and mode of inheritance of the supposed new type, and (2) on the possibility that either WG9 or some other plant of the cultures of 1906 brought the character into the cultures. We shall now consider somewhat extensive evidence bearing on these points, concluding with a special test of the possibility of vicinism.

When I last saw the warm-house plants of 1906, three were known to be singles, and all but two of the rest were recorded as certainly or probably doubles. Seed was secured from these three singles only, and presumably no other singles occurred in the house. Since this seed was all from unguarded flowers, we must consider the possibility that WS1 or WL10, the other warm-house singles, brought the early factor into the cultures. It is also barely possible that pollen was brought to WG9 from some plant not in this greenhouse.

These two parents were tested in supplementary cultures, in house C in 1907, and in house W in 1908. The 1907 progeny averaged slightly earlier than those of other parents, but this may have been due to their position, which was much nearer a partition separating the house[10] from a warm greenhouse. Unfortunately the internodes were not recorded.

In the 1908 cultures these lots were potted two days later than most of the other lots and one day later than the WG9 lot, and for some unknown reason the WL10 lot wilted badly for some days. The parents in question gave singles (16 and 11 plants respectively) which when compared with progeny of CG2 and WG9 (23 and 15) might suggest that the parents were heterozygous for the early type. The results with the similar numbers of doubles decidedly disagree with these, and suggest that cultural accidents produced the differences; the WS1 lot was not exceptional, while all the WL10 progeny were grouped near the lower end of the range of the other lots. In view of all the facts, the data hardly deserve tabular presentation, but they raise a question requiring further study; a later test is reported below.

[10] A temporary substitute for the regular house C.

TABLE 7

1910, greenhouse. Ancestral data and numbers of progeny available for frequency-polygon constants.

Lot	Ancestry [a]			Parental internodes		Numbers of progeny [b]	
	Generation 1	Generation 2	Generation 3	Parent-lot mean	Parental value	Single	Double
1		C1 (Snowflake)	M3 (Snowflake)	32.4	35	7	6
2			M9 (Snowflake)		30	9	5
3		C10 (Early)	C2 (Early)	21.4	16	8	6
4			C5 (Early)		20	8	6
5			C1 (Snowflake)		27	7	7
6		C5 (Snowflake)	M6 (Snowflake)	36.0	33	7	7
7			M9 (Snowflake)		39	4	10
8		C10 (Early)	M4 (Early)	27.3	21	6	8
9	WG9 (Snowflake)		M2 (Early)		25	6	8
10			M7 (Snowflake)		34	3	10
11		C9 (Snowflake)	C3 (Snowflake)	28.5	27	9	5
12			C7 (Snowflake)		29	5	8
13		C10 (Early)	W6 (Early)	42.6	33	8	4
14			W5 (Early)		42	7	7
15			W10 (Snowflake)		55	5	8
16		C9 (Snowflake)	M5 (Snowflake)	34.0	38	6	8
17			M8 (Snowflake)		33	7	5
18	CG2 (Snowflake)	C2 (Snowflake)	C6 (Snowflake)	27.25	27	4	10
19		W4 (Snowflake)	W3 (Snowflake)	54.6	54	6	4
20		syn3 (Snowflake)	C17 (Snowflake)	?	?	7	6
21			M10 (Snowflake)	33.6	25	7	6
22			M11 (Snowflake)		33	6	7
23	WG9 (Snowflake)	$C_2$28 (Smooth-leaved)	.....	30.4	42	7	7
24		W2 (Snowflake)	M7 (Smooth-leaved)	36.2	41	4	7
25		C10 (Early)	C10 (Crenate-leaved)	21.4	19	3	10
26		W2 (Snowflake)	W2 (Crenate-leaved)	47.5	43	6	9
27		W7 (Snowflake)	C5 (Slender)	29.8	25	3	12
28	WS1 (Snowflake)	$W_2$16 (Snowflake)	.....	49.1	38	7	7
29		$W_2$25 ("Bushy")			34	3	8
30	WL10 (Snowflake)	$W_2$20 ("Late, many-noded")	.....	48.6	73	9	1

[a] Seed from bagged flowers except with lots 20 and 23. Parental type determined partly by the progeny tests to be reported. The last two parents gave only Snowflake progeny, aside from one apparent mutant from the former parent.

[b] Excluding several plants not producing flowers on the primary axis.

In the cultures of 1910 and 1911F, all the 1908 progeny of WG9–C10 were tested. On account of the variable nature of the quantitative character involved, an elaborate study was necessary. Only small cultures could be grown in the greenhouse; these were supplemented by larger lots in the field in 1911, but inhibition of flowering by the hot summer, together with the effects of disease and soil variations, made the field results erratic and necessitated special methods of treatment of the evidence.

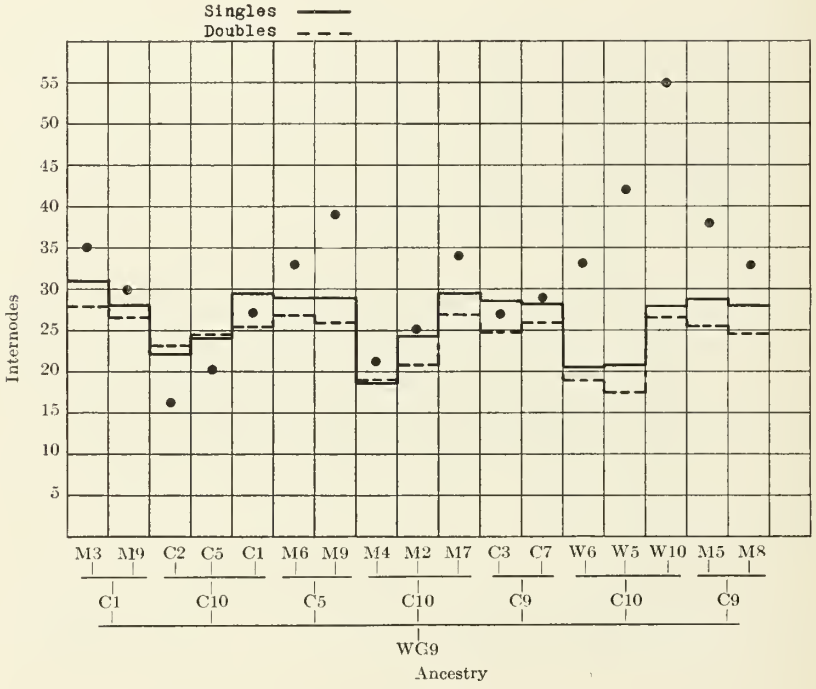

Chart 1. Cultures of 1910. Internodes: parental values and progeny means (respectively shown by dots and lines) for progeny lots 1 to 17, omitting aberrant progeny. Parental values should be compared only for the same house.

Table 7 gives the available data for the parents of the 1910 cultures, and the numbers of progeny available for quantitative data. The order of the pedigree numbers here is the same as that of the progeny lots on the greenhouse bench. For convenience, the 1910 tests of other mutant types, together with tests of several Snowflake parents, are included in the table (lots 18 to 30).

The plants were grown in house C of the previous work. Two or three plants (one shown in fig. 25) were extremely vigorous, presumably because of some accidental soil difference; aside from these, a few apparent mutants, and a few plants otherwise abnormal, the plants were fairly uniform except where heterozygosis was to be expected.

The data for time of flowering, as with the 1908 cultures, show the same main features as the internode data, and only the latter will be considered in detail. The types were again more widely different in internodes than in earliness, a fact which seems to indicate that the early type grows more slowly than Snowflake.

So large and so regular are the differences in internodes that the means of these very small lots seem worthy of presentation (chart 1).[11] Apparently the few-noded character was carried, among the nine parents descended from WG9–C10, by all except the three parents having the highest numbers in their respective houses.

Tables 8 and 9 give the internode frequencies for the singles and doubles respectively, by separate progeny lots and by groups of similar ancestry. The range of variation for the check lots, omitting the indicated apparent mutants and other apparently abnormal plants, is rather surprisingly small, as is the case with the cool-house cultures of 1908. The three late progeny of WG9–C10 give lots closely corresponding in range to the check lots, only one individual falling below the range of the combined check lots. The six early and medium progeny of WG9–C10, on the other hand, give distributions of far greater range than do the check parents, extending to much lower values.

Tables 10 and 11 give the ordinary statistical constants for the grouped lots. The mean number of internodes, for both singles and doubles, is about 25 per cent lower in the progeny of the six few-noded parents, the difference being not far from ten times as great as its probable error. The increase in variability with the progeny of the early parents is also striking, and the difference is about five to six times its probable error. With time to flowering, it may be noted, the differences are similar to those with internodes, but somewhat less marked in the case of the mean; the flowering data are not given here.

It is plain that the previous conclusion as to the heterozygous nature of WG9–C10 is sustained. The elimination of the apparent mutants

[11] Calculated with the apparent mutants and four other apparently abnormal plants eliminated; see tables 8 and 9.

TABLE 8

1910, greenhouse. Number of main-stem internodes below first flower-bearing node. Frequency distributions for singles.[a]

Ancestry	Gen. 1	WG9																				CG2, WS1, WL10 & WG9	
	Gen. 2	C1		C10			C5		C10			C9		C10			C9		C10	C10		Late	Various[b]	All tested
	Gen. 3	M3	M9	C2	C5	C1	M6	M9	M4	M2	M7	C3	C7	W6	W5	W10	M5	M8	C10	Not late	Late	Late	Rest	All tested
Internodes																								
16		....	....	....	....	....	....	....	....	....	....	....	....	....	1	....	....	....	....	1	....	....	.....	1
17		....	....	1	1	....	....	....	....	....	....	....	....	1	....	....	....	....	....	3	....	....	.....	3
18		....	....	1	....	....	....	....	2	....	....	....	....	1	1	....	....	....	....	5	....	....	.....	5
19		....	....	2	1	....	....	....	2	1	....	....	....	2	2†	....	....	....	....	10†	....	....	.....	10
20		....	....	1	1	....	....	....	1†	....	....	....	....	1	....	....	....	....	....	4†	....	....	.....	4
21		....	....	....	....	....	....	....	....	....	....	....	....	....	1	1	....	....	1	1	1	....	2	4
22		....	....	....	....	....	....	....	....	1	....	....	....	1	....	....	....	....	1	2	....	....	1	3
23		....	....	....	1	....	....	....	....	....	....	....	....	1†	....	....	....	....	....	2†	....	....	1	3
24		....	....	1	....	....	....	....	1†	....	....	....	....	....	1	....	....	....	....	3†	....	....	1	4
25		....	....	....	....	....	....	....	....	1	....	....	....	....	....	....	....	....	....	1	....	....	.....	1
26		....	1	....	....	....	....	....	....	2	....	....	1	....	....	....	....	1	....	2	....	3	4	9
27		....	....	....	....	....	....	1	....	....	....	1	....	....	1	....	....	2	....	1	....	4	8	13
28		....	....	....	....	....	2	....	....	1	....	2	....	....	....	1	3	2	....	1	1	9	14	25
29		....	4	1	1	6	3	2	....	....	2	4	3	1	....	1	2	1	....	3	9	19	12	43
30		1	....	1	....	....	2	....	....	....	....	2	....	....	....	....	1	1	1	1	....	7	13	21
31		2	3	....	2	....	....	1	....	....	1	....	....	....	....	2	....	....	....	2	3	6	3	14
32		1	....	....	....	1	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1	1	3	5
33		....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	2	2
34		1*A*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1*A*	2	3

[a] The daggers indicate the position and number of apparent mutants. *A* indicates diseased, injured, or otherwise abnormal individuals. These indications are omitted from the last two columns.

[b] This column includes lots 18 to 30, largely progeny of parents tested as possible mutants; see tables 12 and 13. WG9–C10–C10 belonged to the crenate-leaved type, and its progeny are therefore included in totals only with the last two columns. Plainly it was heterozygous for earliness.

TABLE 8—(*Continued*)

1910, greenhouse. Number of main-stem internodes below first flower-bearing node. Frequency distributions for singles.[a]

Ancestry	Gen. 1	WG9																				CG2, WS1, WL10 & WG9	
	Gen. 2	C1		C10		C5		C10			C9		C10			C9		C10	C10		Late	Various[b]	All tested
	Gen. 3	M3	M9	C2	C5	C1	M6	M9	M4	M2	M7	C3	C7	W6	W5	W10	M5	M8	C10	Not late	Late	Late	Rest	All tested
	Internodes																							
	35	1*A*	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1*A*	.....	1
	36	....	....	....	....	....	....	....	....	....	....	....	1†	....	....	....	....	....	....	....	....	1†	1	2
	37	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	...	... ...	.....
	38	....	1†	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1†	1	2
	39	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	..	1	1
	40	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1	1
	41	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1	1
	42	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	... ...	... ...
	43	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	.....	.....
	44	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1	1
	45	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	.....	... ...
	46	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	.....	... ...
	47	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	.....	.....
	48	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	.....	....
	49	1†	....	....	1†	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1†	....	1†	.....	2

[a] The daggers indicate the position and number of apparent mutants. *A* indieates diseased, injured, or otherwise abnormal individuals. These indications are omitted from the last two columns.

[b] This eolumn includes lots 18 to 30, largely progeny of parents tested as possible mutants; see tables 12 and 13. WG9–C10–C10 belonged to the crenate-leaved type, and its progeny are therefore included in totals only with the last two columns. Plainly it was heterozygous for earliness.

TABLE 9

Same as table 8, for doubles.[a]

Ancestry																							
Gen. 1	WG9																					CG2, WS1, WL10 & WG9	
Gen. 2	C1		C10			C5		C10			C9		C10			C9		C10	C10		Late	Various	All tested
Gen. 3	M3	M9	C2	C5	C1	M6	M9	M4	M2	M7	C3	C7	W6	W5	W10	M5	M8	C10	Not late	Late	Late	Rest	All tested
Internodes																							
14	....	....	....	....	....	....	....	....	....	....	....	....	1	....	....	....	....	....	1	....	....	.....	1
15	....	....	....	....	....	....	....	....	....	....	....	....	....	3	....	....	....	....	3	....	....	.....	3
16	....	....	....	....	....	....	....	....	2	....	....	....	....	1	....	....	....	1	3	....	....	1	4
17	....	....	....	....	....	....	....	2	2	....	....	....	....	....	....	....	....	2	4	....	....	2	6
18	....	....	1	....	....	....	....	3	....	....	....	....	1	....	....	....	....	....	5	....	....	.....	5
19	....	....	....	1	....	....	....	1	....	....	....	....	....	1†	....	....	....	....	3†	....	....	1	4
20	....	....	....	....	....	....	....	....	....	....	....	....	....	1	....	....	....	....	1	....	....	.....	1
21	....	....	....	....	....	....	....	1	....	....	....	....	....	....	....	1	....	3	1	....	1	3	5
22	....	....	1	1	1	....	....	1	1	....	1	....	....	....	....	....	1	2	4	1	2	5	12
23	....	....	....	....	....	....	....	....	....	1	....	....	....	1	....	....	1	....	1	1	1	8	11
24	....	....	2	....	....	....	....	....	....	....	....	....	1A	....	....	1	....	....	3A	....	1	7	11
25	1	....	....	2	1	....	1	....	1	2†	2	1	1	....	1	2	2	2	4	4†	9	15	32
26	....	2	....	....	3	2	7	....	1	1	1	5	....	....	3	1	1	....	1	7	19	11	38
27	2	2	....	1	2	4	1	....	1	5	1	2	....	....	3	3	....	....	2	10	15	16	43
28	1	....	1	....	....	1	....	....	....	....	....	....	....	....	....	....	....	....	1	....	2	11	14
29	1	....	....	1	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1	....	1	6	8
30	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1	....	....	....	....	1	....	3	4
31	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	.....	.....
32	1	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1	3	4
33	....	....	1†	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1†	....	....	.....	1
34	....	....	....	....	....	....	....	....	....	1	....	....	....	....	....	....	....	....	....	1	....	2	3
35	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	.....	.....
36	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	.....	.....
37	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	.....	.....
38	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	.....	.....
39	....	1†	....	....	....	....	1A	....	....	....	....	....	....	....	....	....	....	....	....	....	2†A	.....	2

[a] See notes to table 8.

TABLE 10

1910, greenhouse. Number of main-stem internodes below first flower-bearing node. Constants of the frequency polygon for all plants producing main-stem flower cluster.

	Ancestry			Number of progeny	Mean	Standard deviation	Coefficient of variation
	Gen. 1	Gen. 2	Gen. 3				
Singles	WG9	Late	Late	54	29.80 ± .32	3.47 ± .22	11.63 ± .77
		C10	Late	15	29.00 ± .42	2.39 ± .29	8.26 ± 1.02
			Early	43	22.56 ± .61	5.91 ± .43	26.21 ± 2.03
	All (4)	Various	Various types	72	29.47 ± .32	4.01 ± .23	13.61 ± .78
	All (4)	All	All	184	27.91 ± .26	5.22 ± .18	18.70 ± .68
Doubles	WG9	Late	Late	54	26.50 ± .27	2.95 ± .19	11.15 ± .73
		C10	Late	25	26.44 ± .29	2.14 ± .20	8.08 ± .78
			Early	39	20.92 ± .49	4.55 ± .35	21.74 ± 1.74
	All (4)	Various	Various types	94	25.78 ± .22	3.22 ± .16	12.49 ± .62
	All (4)	All	All	212	25.15 ± .18	3.91 ± .13	15.55 ± .52

TABLE 11

Same as table 10 except for omission of aberrant individuals and mixed groups.[a]

	Ancestry			Number of progeny	Mean	Standard deviation	Coefficient of variation
	Gen. 1	Gen. 2	Gen. 3				
Singles	WG9	Late	Late	49	28.92 ± .13	1.37 ± .09	4.73 ± .32
		C10	Late	15	29.00 ± .42	2.39 ± .29	8.26 ± 1.02
			Early	38	21.97 ± .49	4.50 ± .35	20.47 ± 1.65
Doubles	WG9	Late	Late	53	26.02 ± .16	1.68 ± .11	6.46 ± .43
		C10	Late	24	26.50 ± .30	2.16 ± .21	8.15 ± .80
			Early	36	20.56 ± .47	4.20 ± .33	20.42 ± 1.69

[a] See notes to table 8.

and the other abnormal plants presumably gives a better comparison as to mean and variability, but the conclusion is the same in either case. The three many-noded (late) parents descended from WG9–C10 give no definite indication of being genetically different from the "check" lots not descended from WG9–C10, while the variability constants are sufficient, taken alone, to make probable the genetic differentiation of the fewer-noded progeny of WG9–C10. Apparently all the fewer-noded progeny of WG9–C10 that were tested—seven, when WG9–C10–C10, a crenate-leaved apparent mutant (tables 12 and 13), is included—were either simplex or duplex for presence of an earliness factor or factors.

The variability of all the thirty progeny lots, taken together, is high, as might be expected, though decidedly below that of the progeny of early parents. This high variability is due only in very small part to the progeny of the five or six supposedly mutant parents; the last thirteen lots, alone, are much less variable than the mixed early lots. The portion of the cultures containing these progeny lots from aberrant parents was conspicuous for irregularity of germination, and, on the whole, a relatively low rate of germination.

A few of the last thirteen lots give more evidence bearing on the origin of WG9–C10. The early WG9–syn3–M10 (tables 12 and 13) gives no evidence of genotypic differentiation from its ordinary sib, WG9–syn3–M11; WS1–$W_2$16, another phenotypically early parent, also failed to transmit earliness to its progeny. CG2–C2–C6, on the other hand, although itself an ordinary plant, shows a rather suspicious tendency to the production of early and few-noded progeny, but better evidence would be required for any positive conclusion. WG9–C10–C10 appears, from the data in tables 12 and 13 and from observation of the flowering of plants of the next generation in the 1911H cultures, to have been heterozygous for the early type, as well as for the crenate-leaved type. We find in this test no definite indication that the early type has appeared elsewhere than in WG9–C10 and its descendants.

The F_2 progeny of WG9–C1, an abnormal plant whose F_1 progeny were unusually and uniformly early but not few-noded, have been included with the other check lots without question. This treatment seems justified by the flowering data, which do not indicate any repetition of the precocious development of the first-generation plants; the peculiarities of the F_1 cultures, if not a mere cultural accident, presumably depended on the very abnormal development of the parent,

TABLE 12

1910, greenhouse, lots 18 to 30. Number of main-stem internodes below first flower-bearing node. Frequency distributions for singles.[a]

Ancestry	Gen. 1	CG2		WG9								WS1		WL10
	Gen. 2	C2	W4	syn (M) 3			$C_2$28	W2	C10	W2	W7	$W_2$16	$W_2$25	$W_2$20
	Gen. 3	C6	W3	C17	M10	M11	.....	M7	C10	W2	C5	.....	.....	.....
	Internodes													
	21	1	.....	.....	.....	.....	.....	.....	1‡	.....	.....	.....	.....	.....
	22	.....	.....	.....	.....	.....	.....	.....	1‡	.....	.....	.....	.....	.....
	23	.....	.....	.....	.....	.....	.....	.....	.....	1‡	.....	.....	.....	.....
	24	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	25	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	26	.....	1	.....	.....	.....	.....	.....	.....	1‡	2‡‡	.....	.....	.....
	27	1	.....	.....	1	.....	.....	.....	.....	1‡	1‡	2	.....	2
	28	1	2	1	.....	1	.....	.....	.....	1‡	.....	4	1	3
	29	.....	.....	1	2	2	1	.....	.....	1	.....	.....	2	3
	30	.....	1	3	3	2	1	1	1‡	1	.....	.....	.....	.....
	31	.....	1	.....	1	.....	1	.....	.....	.....	.....	.....	.....	.....
	32	.....	.....	.....	.....	.....	1	1	.....	.....	.....	1	.....	.....
	33	.....	1	.....	.....	1†	.....	.....	.....	.....	.....	.....	.....	.....
	34	.....	.....	1	.....	.....	1	.....	.....	.....	.....	.....	.....	.....
	35	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	36	.....	.....	.....	.....	.....	1	.....	.....	.....	.....	.....	.....	.....
	37	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	38	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1
	39	.....	.....	.....	.....	.....	.....	1‡	.....	.....	.....	.....	.....	.....
	40	.....	.....	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	41	.....	.....	.....	.....	.....	1‡	.....	.....	.....	.....	.....	.....	.....
	42	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	43	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	44	.....	.....	.....	.....	.....	.....	1‡	.....	.....	.....	.....	.....	.....

[a] See table 7 and notes to tables 5 and 8.

TABLE 13

Same as table 12, for doubles.[a]

Ancestry	Gen. 1	CG2		WG9								WS1		WL10
	Gen. 2	C2	W4	syn (M) 3			$C_2$28	W2	C10	W2	W7	$W_2$16	$W_2$25	$W_2$20
	Gen. 3	C6	W3	C17	M10	M11	.....	M7	C10	W2	C5	.....	.....	.....
	Internodes													
	16	.....	.....	.....	.....	.....	.....	.....	1	.....	.....	.....	.....	.....
	17	.....	.....	.....	.....	.....	.....	.....	2	.....	.....	.....	.....	.....
	18	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	19	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	20	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	21	.....	.....	.....	.....	.....	.....	.....	3	.....	.....	.....	.....	.....
	22	1	.....	.....	.....	2	.....	.....	2	.....	.....	.....	.....	.....
	23	.....	1	.....	2	.....	.....	1‡	.....	.....	.....	3††	1	.....
	24	2	1	.....	.....	.....	.....	1‡	.....	1†	.....	.....	2	.....
	25	4	.....	.....	.....	1	3‡‡	.....	2	1‡	1‡	1	1	1
	26	2	.....	2	2	1	.....	.....	.....	1	.....	2	1†	.....
	27	.....	2	.....	1	2	2	.....	.....	3	3	1	2	.....
	28	.....	.....	1	.....	1	1	.....	.....	2	5	.....	1	.....
	29	.....	.....	2	1	.....	1	.....	.....	.....	2	.....	.....	.....
	30	.....	.....	.....	.....	.....	.....	3‡‡	.....	.....	.....	.....	.....	.....
	31	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	32	.....	.....	1	.....	.....	.....	1	.....	.....	1‡	.....	.....	.....
	33	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	34	.....	.....	.....	.....	.....	.....	1	.....	1	.....	.....	.....	.....

[a] See table 7 and notes to tables 5 and 8.

with its aborted main axis and very late production of a flowering shoot.

Table 14 shows the general plan of the house-sown field cultures of 1911. The progeny of WG9–C10 were arranged as before in the order of their numbers of internodes for each house of the 1908 cultures, beginning with the lowest numbers. The parental values for flowering and internodes are the values indicated by "‡" in tables 5

TABLE 14

1911; field, plants transplanted from greenhouse. Ancestry, seed, and numbers of progeny.[a]

Lot	Ancestry			Seeds sown	Number of plants alive 33 days after sowing	Numbers of plants for data on mutation and flowering		
	Gen. 1	Gen. 2	Gen. 3			Total[b]	Singles	Doubles
1	WG9	C5	C8	80	79	77	34	43
2			C10	71	71	70	36	34
3		C10	C2	80	80	79	39	39
4			C5	80	79	78	40	38
5			C8	80	79	78	35	43
6			C1	80	78	76	36	40
7		C5	W18	80	79	77	37	40
8			W24	80	76	75	41	34
9		C10	M4	80, *26*	77	76	30	45
10			M9	80	80	78	36	41
11			M6	80, *63*	77	77	34	42
12			M2	80, *71*	78	77	36	40
13			M7	80	80	80	37	42
14			M8	80	74	70	33	37
15		C9	C3	80	78	78	30	48
16			C7	80	76	75	32	43
17		C10	W6	80	74	70	31	39
18			W4	80, *21*	70	65	26	38
19			W11	80	78	76	34	42
20			W9	80, *19*	76	72	24	47
21			W5	80	79	75	33	42
22			W8	80, *14*	76	74	36	36
23			W7	80	75	72	32	40
24			W3	80	73	71	37	34
25			W10	74	72	66	32	34
26		C10	.....	80	60	59	27	32
27		C9	W10	80	74	73	33	39
28			W24	80	80	78	32	45

[a] For plan of arrangement and parental data, see page 86 and tables 5 and 6. Seeds from unguarded flowers are indicated by italic figures; where two numbers are given the first is the total.

[b] Including twelve plants (all late mutants) with which determination of the form of flower was impossible.

and 6, in the order there given, except that the arrangement by internodes reverses the two-day difference in earliness of the parents of lots 19 and 20; for convenient comparison, the parental and parent-lot internode values are included in table 19.

Two progeny lots were set in each of the fourteen rows; probably the soil was less favorable at the east end of the plot, and hence for the even-numbered lots, at least in about the last seven rows out of the fourteen.

The plants were beginning to grow very rapidly when moved to the field. On account of deficient soil moisture and excessive heat, the transplanting was slow and in part purposely delayed, covering a period of five days. Lots 21 to 28 were set three days later than lots

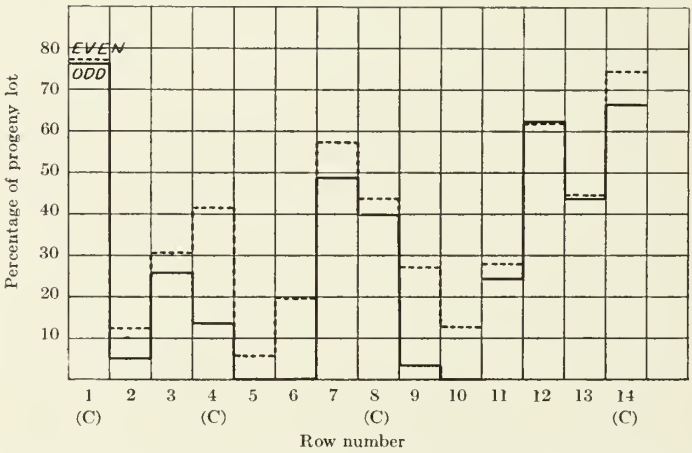

Chart 2. 1911, field; lots transplanted from greenhouse. Percentages of progeny lots not flowering by November 3, for singles. Apparent mutants and injured plants eliminated. Odd-numbered lots represented by solid line. (*C*) indicate check rows. The curves are broken between rows 10 and 11, where a cultural difference enters.

11 to 20, and the later loss of roots resulting seems, in spite of rain coming the next day, to have seriously delayed flowering. Lots 1 and 2 wilted badly after transplanting, and some difference in soil conditions in the flats, rather than a genetic difference, was doubtless responsible for the exceptional lateness of these lots. Lot 20 lost an exceptionally large leaf area as a result of transplanting. A fungus disease (a slow stem rot) was more common on lots 20 to 24 than elsewhere; it doubtless killed some young plants and delayed or prevented flowering in some other cases. Possibly the soil was poorer in the later rows.

TABLE 15

1911, field; plants transplanted from greenhouse. Plants alive November 3, not having flowered. Singles.

Row	Lot	Non-flowering plants	Non-flowering, Snowflake and early types[a]	Lot	Non-flowering plants	Non-flowering, Snowflake and early types[a]
1	1	27	26	2	29	28 (27)
2	3	5	2	4	7	5
3	5	9	9	6	11	11
4	7	7	5	8	17	17
5	9	0	0	10	2	2 (1)
6	11	1	0	12	9	7
7	13	19	18 (17)	14	20	19
8	15	12	12	16	14	14
9	17	1	1	18	8 (7?)	7 (6?)
10	19	0	0	20	3	3
11	21	8	8	22[b]	11	10
12	23	21	20	24	23	23
13	25	16	14 (12)	26	14	12
14	27	23	22	28	24	24

[a] Omitting non-flowering apparent mutants. For the numbers in parenthesis, "doubtful mutants" are classed as mutants. Two plants accidentally seriously injured, in lots 14 and 25, were counted out with the mutants.

[b] The stem-rot disease (see p. 108) was evidently worst in lot 22; some two or three of the worst infected plants (included above) were nearly or quite dead by November 3.

TABLE 16

Same as table 15, for doubles.

Row	Lot	Non-flowering plants	Non-flowering, Snowflake and early types[a]	Lot	Non-flowering plants	Non-flowering, Snowflake and early types[a]
1	1	4	2	2	0	0
2	3	3	1	4	1	1 (0)
3	5	3	3	6	0	0
4	7	3	2 (1)	8	3	1
5	9	2	0	10	0	0
6	11	0	0	12	0	0
7	13	4	2 (1)	14	1	1
8	15	2	2	16	6	5
9	17	1	0	18	3	3 (2)
10	19	0	0	20	2	2
11	21	3	1	22	1	1
12	23	5	5	24	4	4
13	25	1	1	26	7	5
14	27	1	1	28	10	8

[a] See notes to table 15.

Altogether, these cultures are doubtless much less reliable for their size than the greenhouse tests of the early type, but they nevertheless, with due consideration of the points just mentioned, seem to permit of fairly safe conclusions for most of the parents.

The plants were examined for flowering every other afternoon from July 4 to November 3, inclusive (73 to 195 days from sowing). A very large part of the plants flowered in July, some in August, and a few still later. Evidently the high summer temperature largely inhibited flowering; many of the singles and a few of the doubles entirely failed to flower.

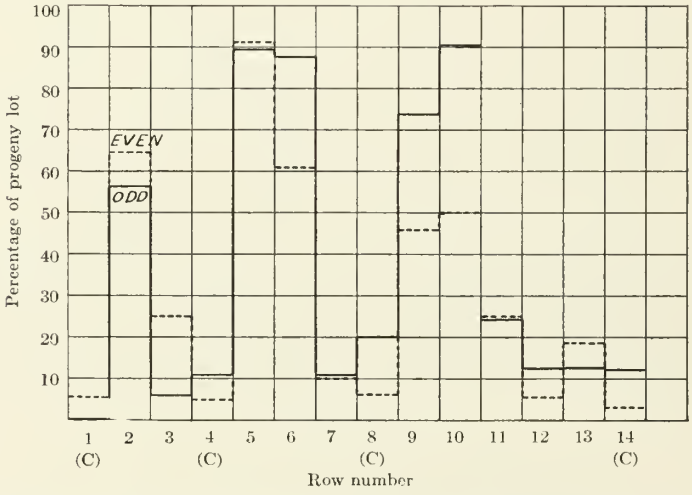

Chart 3. 1911, field; lots transplanted from greenhouse. Percentages of progeny lots with primary cluster flowering or aborted by October 10–16, for singles. Lines as in chart 2.

Figures 5 and 6 show the plants in July. Growth was usually vigorous through the season, but the internodes were very short, the branches numerous, and the region of the terminal inflorescence often abortive, so that determination of the number of main-stem internodes was not practicable. The emergence of the earliest corolla on the plant was recorded at the bi-diurnal observations, and at two periods during the season the aborted primary clusters were noted.

The data show very definitely the transmission of "earliness" by the fewer-noded progeny of WG9–C10. Tables 15 and 16 show the numbers of plants alive, without having flowered, on November 3; the figures are thus a measure of lateness. The two progeny lots in each row are given one line in each of the tables, in order to facilitate separate comparison of the fourteen lots in each end half of the plot.

The last column, with the apparent mutants omitted, no doubt gives the best comparison. The data for the singles, reduced to percentages, are also given in chart 2.

The doubles, which are often earlier to flower than the singles under unfavorable climatic conditions, flowered so generally that table 16 presents no significant differences. The singles (table 15), however, give definite evidence of segregation; the lots in rows 2, 5, 6, and 9 to 11 all show a tendency to early flowering. Lot 26, consisting of F_1

TABLE 17

1911, field; plants transplanted from greenhouse. Singles with primary inflorescence flowering or aborted as indicated.[a]

Row	Lot	Aborted by July 29	Flowering or aborted by Oct. 10–16	Lot	Aborted by July 29	Flowering or aborted by Oct. 10–16
1	1	0	0	2	0	0 (2)
2	3	12 (13)	19 (22)	4	20	24 (26)
3	5	2	2	6	4	8 (9)
4	7	2 (3)	3 (4)	8	1	1 (2)
5	9	22	27	10	26	33
6	11	25	29 (30)	12	17	22
7	13	1	2 (4)	14	2 (3)	2 (3)
8	15	4	5 (6)	16	0 (1)	1 (2)
9	17	19 (20)	20 (23)	18	9	12
10	19	25 (27)	29 (31)	20	11	12
11	21	4	6 (8)	22	7	9
12	23	2	3 (4)	24	1	1 (2)
13	25	0	3 (4)	26	3	4 (5)
14	27	1	3 (4)	28	0	0 (1)

[a] In this table and also in table 18 the numbers in parenthesis include the probable but somewhat doubtful cases.

progeny of WG9–C10, is decidedly earlier than the adjacent lots. Lot 25 also appears early, however.

Tables 17 and 18 give a direct measure of earliness, relating to the primary inflorescence alone. The clusters visibly aborted were in general relatively far advanced, and those aborted at the earlier date correspond to decidedly early flowering; consequently the flowering and aborted clusters are classed together as early. Chart 3 gives the percentages for singles.

Here the data for the doubles show fairly consistent differences in the number aborted at the earlier date, while the October totals are

less regular. There are contrasts similar to those of table 15 up to lot 26, which is late, while the check lots 27 and 28 are early. The singles show the type differences very strikingly throughout lots 1 to 20, while lots 21, 22, and 26 give less positive indications of the presence of the early factor.

Table 19 gives the numbers of singles flowering, in primary inflorescence or elsewhere, by November 3, when growth had practically stopped. The indications are in general the same as with the data already discussed, with better evidence than usual that lots 21 and 22

TABLE 18

Same as table 17, for doubles.[a]

Row	Lot	Aborted by July 29	Flowering or aborted by Oct. 10–16	Lot	Aborted by July 29	Flowering or aborted by Oct. 10–16
1	1	15	30	2	6	22 (23)
2	3	23	33 (34)	4	21	35
3	5	12	29 (30)	6	16	30 (31)
4	7	17	30	8	8	22 (24)
5	9	25	41	10	24	41
6	11	25 (26)	40 (41)	12	23	40
7	13	16	28	14	22	31
8	15	27	37 (39)	16	11 (12)	29 (32)
9	17	20	35	18	20 (21)	32 (33)
10	19	21	41 (42)	20	21	42 (44)
11	21	22	35	22	18	27 (28)
12	23	16 (17)	27 (28)	24	10	16 (17)
13	25	17	25	26	9	15
14	27	21	29 (30)	28	20	25 (27)

[a] See note to table 17.

possessed the early factor. The mean time of flowering is irregular, but shows some effect of the earliness factor. Lot 26 is late as to number flowering, but early as to mean.

Table 20, for doubles flowering by August 1, no doubt gives more reliable means; these means disagree with our scheme only in lot 26 and perhaps lot 22.

According to tables 17–20, the fewer-noded check parent of each check row has usually given the earlier progeny. In fact, the agreement of parental and progeny differences, throughout the cultures, is decidedly remarkable. It is unfortunate that the later parents were always placed in the east half of the row, especially in view of the fact that there was indication of important differences in soil and

TABLE 19

1911, field; plants transplanted from greenhouse. Time from sowing to emergence of earliest corolla. Singles.

Row	Parent-lot internode mean	Lot	Parental internode number	Progeny flowering by Nov. 3		Lot	Parental internode number	Progeny flowering by Nov. 3	
				Number	Days to flowering			Number	Days to flowering
1	29.60	1	29	7	147.14	2	32	7	128.57
2	21.40	3	16	34	91.94	4	20	33	105.45
3		5	25	26	119.46	6	27	25	104.08
4	49.57	7	46	30	103.13	8	54	24	105.67
5		9	21	30	91.73	10	21	34	91.12
6	27.33	11	22	33	98.85	12	25	27	108.30
7		13	34	18	100.67	14	41	13	120.62
8	28.50	15	27	17	112.94	16	29	18	118.00
9		17	33	30	100.27	18	35	18	109.67
10		19	36	34	97.35	20	37	21	117.81
11	42.56[a]	21	42	25	129.36	22	45	25	121.76
12		23	49	11	122.00	24	51	14	151.57
13		25	55	15	136.40	26	....	13	121.08
14	47.80	27	46	10	159.40	28	56	8	162.50

[a] This parent-lot value does not apply to lot 26, which consists of progeny of WG9–C10 itself.

TABLE 20

Same as table 19, for doubles flowering by August 1.

Row	Lot	Progeny flowering by Aug. 1[a]		Lot	Progeny flowering by Aug. 1	
		Number	Days to flowering		Number	Days to flowering
1	1	38	90.26	2	33	91.03
2	3	36	80.22	4	36	80.00
3	5	39	84.46	6	39	84.10
4	7	36	81.28	8	31	84.32
5	9	42	75.86	10	41	76.59
6	11	42	77.90	12	40	80.25
7	13	37	84.32	14	35	84.80
8	15	46	83.87	16	33	85.21
9	17	37	80.43	18	34	84.12
10	19	42	78.24	20	39	83.85
11	21	39	85.95	22	30	87.93
12	23	33	89.03	24	26	88.85
13	25	32	88.56	26	21	89.05
14	27	35	88.97	28	29	90.28

[a] Only 48 more doubles altogether flowered by November 3, and 25 of these were in the even-numbered lots 20 to 28.

probably in the incidence of disease, favoring the plants in the west half. The internode data of 1910, however, show a similar tendency. Small genetic differences are suggested, though it would be remarkable if they were so uniformly present in these plants of a single line of a usually selfed species, descendants of parents and a common grandparent grown under glass.

If such differences exist in the race, conceivably some combination due to crossing might simulate an early mutation. The evidence as a whole, however, does not favor such an origin for our early type; it is widely divergent from the Snowflake type, and seems to depend on a single main factor difference from Snowflake.

TABLE 21

Cultures of 1912. Ancestry and parental data.

Lot	Parent	Parental data			Seeds sown
		Probable type	Days to flowering[d]	Internodes[d]	
1	WS1–$W_2$16	Snowflake[a]	120.5	38	15
2	WG9–C10–W6	Early	116.5	33	15
3	WL10–$W_2$2	Snowflake	139.5	51	15
4	WL10–$W_2$3	Snowflake[a]	120.5	38	15
5	WS1–$W_2$1	Snowflake	141.5	57	15
6	WL10–$W_2$14	Snowflake[a]	126.5	38	15
7	WL10–$W_2$7	Snowflake	145.5	54	15
8	WG9–C10–W8	Early	129.5	45	15
9	WS1–$W_2$12	Crenate-leaved[a,b]	119.5	34	7[c]

[a] Suspected before testing of belonging to the early type; first parent also tested in 1910.

[b] A heterozygote between the crenate-leaved and Snowflake types.

[c] Probably open pollinated.

[d] All the parents grew in the same house at the same time.

The essential feature of the supplementary cultures of 1912, since no seed of WL10 remained, was a test of two pairs of early and late progeny of WL10 (lots 3 and 4, 6 and 7, table 21), in comparison with two control lots—one (lot 2) from a known early parent, descended from WG9–C10, and one (lot 5) from a late descendent of WS1. Incidentally, WS1–$W_2$16 and WG9–C10–W8 were retested, and the few available seeds of WS1–$W_2$12 were used to test that phenotypically early parent.

The results are given in tables 22 and 23 and chart 4. The very low individual from WS1–$W_2$16 came from a very weak embryo, and should be disregarded; the exceptionally high general range of this lot, which was also visibly behind all others in development, was prob-

TABLE 22

Cultures of 1912. Number of main-stem internodes below first flower-bearing node. Frequeney distributions for singles.[a]

Ancestry										
	Gen. 1	WS1	WG9	WL10		WS1	WL10		WG9	WS1
	Gen. 2	$W_2$16	C10	$W_2$2	$W_2$3	$W_2$1	$W_2$14	$W_2$7	C10	$W_2$12
	Gen. 3		W6						W8	
Internodes										
18									1†	
19			1							
20									1	
21										
22			1							
23			3							
24									2	
25										
26		1†			1	1				
27			1	1		3	2			
28				4	1	3	1	3	1	1‡
29		1		1		1	2	2		1‡
30		2					1			
31		1								
32										
33										
34										
35		2†								

[a] See note *a* to table 5.

TABLE 23

Cultures of 1912. Same as table 22, for doubles.[a]

Ancestry										
	Gen. 1	WS1	WG9	WL10		WS1	WL10		WG9	WS1
	Gen. 2	$W_2$16	C10	$W_2$2	$W_2$3	$W_2$1	$W_2$14	$W_2$7	C10	$W_2$12
	Gen. 3		W6						W8	
Internodes										
12		1A								
13										
14										
15										
16										
17									1	
18			1							
19			1							
20			1				1			
21			2					1	2	
22		1	2					1	2	
23			1		1†			1		
24				1	3		1	1		
25				5	3	2	3	2	1	1
26				1	2	3	1	3	2	1
27		2								
28		3†								1†
29										
30			1							
31						1				

[a] See note *a* to table 5.

ably due to some cultural accident, perhaps to an excess of moisture in this row of pots.

The lots of plants may seem rather absurdly small for their purpose, but the uniformity of development here, with the marked normal divergence in internodes of the types in question, seems to justify a fair degree of confidence. Ten plants here were probably worth fifty in the field.

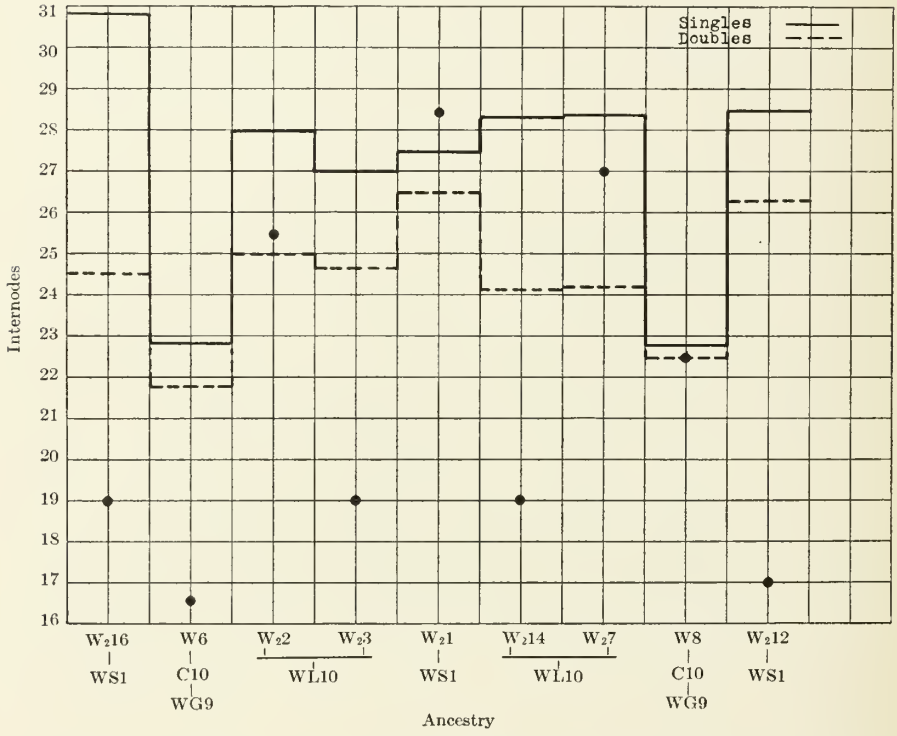

Chart 4. Cultures of 1912. Internodes: parental values and progeny means, shown as in chart 1. The true parental values are twice those indicated by the ordinate figures, which apply directly to the progeny values.

This test, with that of 1910, shows very positively that WS1–$W_2$16 was only phenotypically few-noded. Evidently WG9–C10–W8, the parent of field lot 22, really carried the earliness factor, as was somewhat doubtfully inferred from the field results; the five progeny of WS1–$W_2$12, on the other hand, though from a fewer-noded parent, have values that make the presence of the earliness factor improbable.

On the main point at issue the evidence seems satisfactory. Neither of the two very early and few-noded progeny of WL10 represented

shows in its progeny any evidence of belonging to the early type; the means are slightly lower than for the many-noded sibs of these parents, but far less so than with the parents descended from WG9–C10.

We conclude, then, that WG9–C10 was probably a monohybrid, and that the early-bearing gamete entering into its composition was of unknown but presumably mutative origin.

Most of the extracted late or many-noded parents may now be selected with practical certainty. WG9–C10–C8 and C1 (lots 5 and 6 in the 1911F cultures) and WG9–C10–M7 and M8 (lots 13 and 14) were genetically very similar to the check parents, as has already been concluded for two of them from the greenhouse cultures; presumably they were pure Snowflake.

The data for WG9–C10 itself (lot 26) seem to indicate that the results from the last eight lots are of very doubtful value; still, they show, especially in the original individual records, some evidence of the earliness factor which must be present in part of the individuals. The poor and slow germination of the old seed available may have had an important influence on the result; many of the early embryos may have been non-viable, and the seedlings may have been weaker than those from fresh seed. The 1911 data and observation of the plants in the field suggest that WG9–C10–W7, W3, and W10 (lots 23, 24, and 25) are the only remaining extracted late parents, WG9–C10–W5 and W8 (lots 21 and 22) carrying the earliness factor, as the four parents just preceding them in the cultures obviously did. Tables 22 and 23 confirm this conclusion for WG9–C10–W8.

It is presumably impossible to make a positive separation of the parents homozygous for the presence of the early factor. The greenhouse data suggest that WG9–C10–M4 was a pure early individual; the field data (see lot 9) agree, and suggest that WG9–C10–M9 (lot 10) and perhaps WG9–C10–M6 (lot 11) belong in the same class. WG9–C10–C2, C5, and C10 (lots 3, 4, and 40)[12] were all evidently heterozygous. Of the parents grown in house W, it would seem that only WG9–C10–W11 (field lot 19) was homozygous early. We have, provisionally, for the available single progeny of WG9–C10:

	House C	House M	House W	Total
Pure early	0	3	1	4
Hybrid early	3	1	5	9
Pure late	2	2	3	7
				20

[12] Statistical data given for the last only for the 1910 cultures, not for this field lot.

This corresponds well enough with the monohybrid expectation of 5 : 10 : 5; in fact, the deviation is just such as would be expected if there was occasional cross pollination of the unprotected flowers of WG9–C10 from Snowflake plants. The large proportion of evidently pure late parents is strong evidence for the monohybrid nature of WG9–C10.

The proportions of the two types among the doubles can only be estimated. The 1908 data suggest that 5 of the 10 doubles there reported were early; this number, with the 13 singles so classed, makes a total of 18 early-type plants out of 30. The ratio is slightly nearer to 1 : 1 than to 3 : 1, and the former proportion would suggest the peculiar type of inheritance found with the mutant types yet to be described. The evidence of the 1910 distributions, however, shows that the early type largely predominates in the next generation with both singles and doubles, and apparently this is true even when we exclude the progeny of the one parent classed as pure early.

The early factor can be positively detected only by progeny tests. No test has shown the presence of this factor elsewhere than in WG9–C10 and part of its descendants. WG9–C10 produced the early and Snowflake types among 20 single progeny nearly in the typical monohybrid proportions. Inspection of the double progeny in two generations suggests similar or possibly somewhat lower proportions there. A vicinistic origin for WG9–C10 is improbable. Presumably, then, the early type arose from Snowflake by a single factor mutation, the dominant mutant factor being inherited without special complications. We shall now consider certain apparently mutant types which are characterized by peculiar genetic behavior.

2. THE SMOOTH-LEAVED TYPE

This type was first observed in the cultures of 1908 (table 1) and has occurred frequently in later cultures (table 3). It is perhaps the mutant type of most frequent occurrence among progeny of Snowflake or early parents; 2410 unselected progeny from house-sown seed of such parents (see table 28) included 28 apparent mutants (14 singles, 11 doubles, and 3 undetermined), a mutation coefficient of $1.16 \pm .15$ per cent.

As grown in the greenhouse at Ithaca, this type (fig. 7, tables 12 and 13) was often many-noded, with correspondingly late flowering. Its most striking peculiarity, shown especially by young seedlings and not evident in the figures, was a lack of buckling between the veins

TABLE 24

Smooth-leaved type: heredity of apparent mutants and their progeny.[a]

Parents	Progeny										
	Cultures	Seeds[b]	Plants								
			Total examined		Smooth-leaved			Snowflake			Other types
			Undetermined	Determined	Single	Double	All	Single	Double	All	
26a	1911F	*123*	0	65	.....	.....	18	.....	.....	44 (46)	(1)
26b	1910 & 1911F	*79*	0	29	1	2	6	6	5	22	1
26c	1910 & 1911F	42, *15*	3	21	2	4	8	2	3	11 (13)	0
All P_1 smooth	All	244, *217*	3	115	3	6	32	8	8	77 (81)	1 (2)
26b-10	1911H	20	0	8	1	0	1	2	4	6	(1)
26c-6	1911H, 1913, 1914	118	2	56	0	2	11	20 (22)	19 (20)	40 (43)	2
26c-8	1911H, 1913, 1914	118	3	55	6	6	19 (20)	12 (13)	16 (18)	28 (31)	1 (4)
All F_1 smooth	All	256	5	119	7	8	31 (32)	34 (37)	39 (42)	74 (80)	3 (7)
All smooth	All	500, *217*	8	234	10	14	63 (64)	42 (45)	47 (50)	151 (161)	4 (9)
26b-4	1911H	20	0	19	.....	.....	0	6	11 (13)	17 (19)	0
26c-3	1913	50	0	41	.....	.....	0	24 (25)	13 (15)	37 (40)	1
26c-8-8	1913	95, *50*	2	73	.....	.....	0	33 (34)	38	71 (72)	1
26c-8-15	1913	23	0	20	.....	.....	0	11 (12)	7	18 (19)	1
26c-14	1911H	20	0	20	.....	.....	0	7 (8)	10	18 (19)	(1)
All Snowflake	All	208, *50*	2	173	.....	.....	0	81 (85)	79 (83)	161 (169)	3 (4)

[a] For an explanation of the plan of this and the following tables, see the statement commencing the discussion of this table.

[b] In each case the first number of seeds is the total planted. The numbers from unguarded flowers are given in italics, and those from doubtfully guarded flowers are marked with an asterisk.

of the leaves, and of general convexity of the upper surface of the leaves. Mature plants developed under favorable conditions in the greenhouse closely resembled Snowflake; the leaves, however, were noticeably brittle, and the dry capsules so brittle that it was often necessary, as it was not with Snowflake, to shell the seeds individually. Probably the fibrovascular system is in some way defective; *Oenothera rubrinervis*, which is also brittle (de Vries, 1906, lecture 18), has thin-walled bast fibers.

In the field cultures, both at Ithaca (fig. 5) and at Riverside, under conditions less favorable on the whole to the initiation of flowering, this type (fig. 8) differed much more widely from Snowflake. Flowering was excessively delayed, and the plants often remained low, with few branches, and rosette-like, with thin, rather narrow leaves. Small brown dead spots, possibly due to excessive transpiration, occurred so frequently on the leaves as to constitute a good diagnostic character for the type. Another peculiarity observed in the field is a reflexed position of the tip of the young leaf when first visible—Snowflake leaves being completely erect from the first.

In the 1914 cultures, with better development than in other field cultures, some smooth-leaved plants (figs. 9 and 10) were again more like Snowflake, though later and evidently more leafy.

Six smooth-leaved parents have been used in progeny tests, three of these being apparent mutants and three being F_1 progeny of two of those mutants. The results are presented in tables 24 and 25; these tables require a brief explanation, which will apply also to the similar tables for other types.

For the plan of the new pedigree numbers here used, see "Methods." The initial plants of a series are designated as the P_1 generation in the tables, their progeny as F_1, etc. In table 24 the cultures are arranged according to their generations and their pedigree numbers under each generation; the smooth-leaved parents (P_1 or of the P_1 type) are given first, followed by the extracted Snowflake parents. In table 25 "good germination" indicates that in all lots included (taken as grown, not as summed by parents in table 24) the number of plants determined exceeds 50 per cent of the number of seeds sown, and *vice versa;* the weighted mean percentages obtained by dividing the total numbers of plants by the respective total numbers of seeds are given for each table in a footnote.

All six smooth-leaved parents (tables 24 and 25) gave mixed progeny, part smooth-leaved and part Snowflake. The surprising

fact is that the parental (smooth-leaved) type appears not in three-fourths of the progeny, but in only about one-fourth.

The extracted Snowflake parents tested behave like pure recessives, showing no influence of their smooth-leaved ancestry. Only the aberrant ratio seems inconsistent with the assumption that the smooth-leaved individuals tested were ordinary heterozygous dominants.

The relatively weak growth of this type and the apparently poor germination of the seed produced by it suggest that normal segregation may be masked by selective elimination. Possibly the smooth-leaved

TABLE 25

Smooth-leaved type: heredity. Summary.

Parents	Progeny					
	Cultures	Seeds	Plants			
			Total examined		Smooth-leaved	
			Undetermined	Determined	Number	Per cent
All smooth-leaved	Ithaca	304, *217*	7	156	40	25.6 ± 2.4
All smooth-leaved	Riverside	196	1	78	23 (24)	30.8 ± 3.4
All smooth-leaved (6)	All	500, *217*	8	234	63 (64)	27.4 ± 2.0
All P_1 smooth-leaved (3)	All	244, *217*	3	115	32	27.8 ± 2.8
All F_1 smooth-leaved (3)	All	256	5	119	31 (32)	26.9 ± 2.8
All smooth-leaved	Germination good	293, *138*	8	187[a]	55 (56)	29.9 ± 2.2
All smooth-leaved	Germination poor	207, *79*	0	47[a]	8	17.0 ± 4.4
All Snowflake (5, F_1 and F_2)	All	208, *50*	2	173	0	0

[a] Respectively 63.8 and 22.7 per cent of the numbers of seeds planted.

factor is lethal when homozygous, as is often the case (Muller, 1918) with dominant mutant factors in *Drosophila;* the data for germination, however, indicate that two-thirds of the mature embryos can hardly belong to the mutant type. We might expect, in view of the weak growth of smooth-leaved plants, that partial elimination of heterozygotes would also occur. That this is the case is suggested, though the numbers are small, by the lower proportion of the mutant type with poor germination (table 25; see also tables 39 and 40); it should be noted, however, that transferring the first lot of table 24, the only lot between 50 and 73 per cent, to the "poor" total, makes the percentages practically identical.[13]

[13] See also table 2 and the second paragraph under "Occurrence of Mutants."

In connection with the question of lethal action we must consider the inheritance of doubleness of flowers. Snowflake seed regularly gives a mixture of singles and doubles, about 53 per cent being doubles. The doubles, which are totally sterile, are probably (Frost, 1915) pure recessives (*dd*) for a single-double factor pair. The singles are always heterozygous (*Dd*); crosses with pure single races (Saunders, 1911) show that the approximately 1 : 1 ratio and the failure to produce pure singles, with self pollination, are due to the fact that all the functional pollen is doubleness-carrying (*d*). The excess of doubles over 50 per cent has been explained by Miss Saunders (1911) as due to heterozygosis of the singles for two linked complementary factors necessary to singleness, and by the present writer (Frost, 1915) as due to lower viability of the "single" gametes or embryos. The absence of functional single-carrying pollen is apparently due to a lethal factor acting after separation of the microspore tetrads, since the tetrads themselves appear normal.

In any consideration of factors linked with the single-double pair, this semisterility of the pollen must be remembered. For example, any dominant factor completely coupled with *D* in pollen formation would be totally absent from the functional pollen, and the zygotes produced by selfing would show directly the strength of linkage in the ovules.

The available data for the smooth-leaved type (table 24) are far from constituting an adequate test of linkage, but they suggest that the factors are independent. Certainly no high degree of linkage is indicated by the totals, nor do the detailed data suggest that smooth-leavedness is coupled with singleness in some parents and with doubleness in others.

We must admit that the peculiar inheritance of this type is not yet positively explained. Evidently larger cultures are needed, and crossing with the Snowflake type and with other commercial varieties; cytological study may also be required. Certain comparisons and speculative possibilities deserve mention, however, especially since the types yet to be discussed furnish additional evidence bearing on them. We may compare the smooth-leaved and double types, as follows:

Double	Smooth-leaved
1. A rare mutation of pure single ("normal").	1. Apparently a common mutation of pure Snowflake ("normal").
2. Recessive; extracted recessives are sterile mutant-type plants.	2. Apparently dominant; extracted recessives are fertile normal plants.

Double	Smooth-leaved
3. Homozygous dominants not produced by hybrids, because functional pollen carries recessive factor only.	3. Homozygous dominants perhaps not produced by hybrids.[14]
4. Recessive (mutant) type the more vigorous.	4. Recessive (normal) type the more vigorous; difference much greater than with single and double.
5. Dominant factor or another factor very closely linked with it is incompatible with formation of functional pollen.	5. Relation of dominant factor to viability of pollen not yet determined.
6. Recessive type exceeds the expected equality by about 3 per cent among some 7000 individuals.	6. Recessive type exceeds equality by about 23 per cent among 234 individuals.

The most probable hypothesis for smooth-leavedness, then, would so far seem to be essentially the same as for doubleness—complete elimination of the weaker type in pollen formation, and partial elimination in embryo-sac formation. Reciprocal crosses with Snowflake are obviously necessary; as we shall soon see, three of the other mutant types *have already proved to be carried by both eggs and sperms.*

The case of *Oenothera lata* (Gates, 1915) suggests the possibility that the smooth-leaved form might arise by reduplication of a chromosome. With ordinary *O. lata* the pollen is sterile, but pollination by *O. lamarckiana* gives about 15–20 per cent of *lata*. This deficiency of *lata* individuals is due, it seems, to a frequent loss of the extra chromosome at meiosis in *lata* ovules, with a resulting formation of more than 50 per cent of seven-chromosome (*lamarckiana*) eggs.

If the smooth-leaved type originates through duplication of a chromosome, we might suppose that other types of similar heredity involve other pairs of chromosomes. The apparent parallel with *O. lata*, which Bartlett (1917) has noted, was long ago suggested by the data, but with at least two or three types to be described linkage phenomena have seemed to conflict with this interpretation. Possibly different processes have produced different mutant types as with *Oenothera;* as we have considered types suggestive of *O. rubrinervis* (early) and of *O. lata* (smooth-leaved), we may consider next a form which in appearance is remarkably suggestive of *O. gigas*.

[14] This possibility is only suggested by these cultures, but it becomes highly probable when the data for other types are considered.

TABLE 26[a]

Large-leaved type: heredity of an apparent mutant and its descendants

Parents	Progeny										
	Cultures	Seeds	Plants								
			Total examined		Large-leaved			Snowflake			Other types
			Undetermined	Determined	Single	Double	All	Single	Double	All	
28a	1913, 1914, & 1915–16	122	2	73	23	14 (16)	38 (40)	13 (14)	12 (17)	25 (31)	2
28a–1	1914	*24*	1	6	0	2 (3)	2 (3)	0	0 (3)	0 (3)	0
28a–8	1914	*48*	0	17	2 (3)	3 (4)	5 (7)	3 (5)	5	8 (10)	0
28a–9	1914	*48*	1	17	1 (2)	5 (6)	7 (9)	2	2 (6)	4 (8)	0
28a–29	1915–16	*24*	0	20	7	2	12	1	7	8	0
28a–37	1915–16	*24*	0	16	1	1 (3)	2 (5)	5	6	11	0
28a–46	1915–16	*24*	0	17	1 (2)	6 (7)	8 (10)	2 (4)	3	5 (7)	0
28a–47	1915–16	*24*	0	13	2	7	9	0	4	4	0
28a–53	1915–16	*24*	0	19	2	3	6	7	6	13	0
28a–55	1915–16	24, 7*	0	14	3	3	6	2	6	8	0
28a–57	1915–16	24, *11*	0	18	1 (2)	1 (4)	2 (6)	2	6 (8)	8 (11)	1[b]
28a–62	1915–16	*24*	2	17	5 (6)	4	9 (10)	1 (2)	4	5 (6)	1
28a–66	1915–16	*24*	0	18	5 (6)	5	10 (11)	4	3	7	0
28a–67	1915–16	*24*	0	20	1 (2)	5 (6)	7 (9)	6	4	10	1
28a–71	1915–16	24, *19*	0	11	2	0	3	5	2	7	1
28a–73	1915–16	24*	0	7	2	0 (1)	2 (3)	2 (3)	1	3 (4)	0
28a–F_1	All	408, 31*, *342*	4	230	35 (42)	47 (58)	90 (109)	42 (48)	59 (68)	101 (117)	4
28a–8–30	1915–16	*24*	0	18	3	3 (4)	8 (9)	5	2 (4)	7 (9)	0
28a–8–38	1915–16	*24*	0	11	3	3	6	3 (4)	1	4 (5)	0
28a–9–2	1915–16	*18*	0	6	0	2	2	3	1	4	0
28a–9–28	1915–16	*24*	0	19	6	3	9	4	5 (6)	9 (10)	0
28a–F_2	1915–16	*90*	0	54	12	11 (12)	25 (26)	15 (16)	9 (12)	24 (28)	0
All large-leaved	All	620, 31*, *432*	6	357	70 (77)	72 (86)	153 (175)	70 (78)	80 (97)	159 (176)	6
28a–75 (Snowflake)	1915–16	24*	0	15	0	0	0	7	8	15	0

[a] See notes to table 24.

[b] Appearing like large-leaved slender.

It should, however, first be noted that, as will appear later, phenomena of apparent linkage in the case of certain other types (crenate, slender, and narrow) suggest that these forms commonly arise from Snowflake by segregation rather than by immediate mutation. The obvious objection to this hypothesis is the fact that the apparently mutant types seem to be dominant to the "normal" or Snowflake type. This objection can be met by assuming the presence of dominant inhibiting factors in the Snowflake parents that give apparent mutants.[15]

If the apparent mutants of the smooth-leaved type are thus produced by crossing over in a set of balanced factors, the lethal "balancing" the smooth-leaved factor itself may be distinct from that which sterilizes the singleness-carrying pollen. In considering the results here reported, therefore, we must always bear in mind the possible presence of several unidentified lethal factors. If the apparent absence of linkage between the smooth and double factors is not misleading, we must suppose that these factors are carried by different pairs of chromosomes; considerations advanced by Muller (1918, pp. 479–482), however, make it rather probable that the commoner types of apparent mutants here discussed are all due to factors carried by one pair of chromosomes, the pair containing the factor for doubleness and its normal allelomorph.

3. THE LARGE-LEAVED TYPE

A double of this type probably occurred in the 1907 cultures, though its appearance attracted so little attention that no record was made. In the field cultures of 1911 (table 3) several individuals suggested a *gigas* type, though there seemed to be intergradation with Snowflake. In the 1912 cultures a single with leaves "long, rather narrow, thick" developed normally and produced an abundance of good seed; from this individual (28a) all cultures of this type are descended.

This type is stout and coarse throughout, and late to flower. The leaves are strikingly long, thick, and rigid, though as a rule relatively

[15] A letter suggesting this explanation was received from Dr. Muller soon after the same idea had been outlined in the "General Discussion" section below. Dr. Muller kindly gave further attention to difficulties at first encountered by the present writer, materially assisting in the formulation of an apparently tenable form of the hypothesis. Since, however, this scheme may seem "far-fetched" and unduly complex, it appears desirable to leave the original discussion of the individual types substantially unchanged. When the difficulties encountered by the assumption of frequent true mutation have been more fully presented, the need for some such addition to the scheme will be more evident.

narrow; under unfavorable weather conditions the flowers are often few and defective, while the leaves are resistant and long-lived (fig. 11). Figures 12 and 13 show well the coarse leaves and lateness of well developed large-leaved plants in the 1915–16 cultures, the plants in the latter figure being several weeks the older.

The results of the progeny tests are given in tables 26 and 27. All the twenty large-leaved individuals tested have given mixed progeny; the proportion of the mutant type, though much larger than with

TABLE 27

Large-leaved type: heredity. Summary.

Parents	Progeny					
	Cultures	Seeds[a]	Plants			
			Total examined		Large-leaved	
			Undetermined	Determined	Number	Per cent
28a	1913, 1914, & 1915–16	122	2	73	38 (40)	54.8 ± 3.9
28a–F_1 (3)	1914	120	2	40	14 (19)	47.5 ± 5.3
28a–F_1 (12)	1915–16	288	2	190	76 (90)	47.4 ± 2.4
28a–F_2 (4)	1915–16	90	0	54	25 (26)	48.1 ± 4.6
28a–F_1 & F_2 (19)	All	498	4	284	115 (135)	47.5 ± 2.0
All large-leaved (20)	All	620	6	357	153 (175)	49.0 ± 1.8
Large-leaved	Germination good	360	3	260[b]	115 (131)	50.4 ± 2.1
Large-leaved	Germination poor	260	3	97[b]	38 (44)	45.4 ± 3.4
Snowflake (1, F_1)	1915–16	24	0	15	0	0

[a] Mainly from unguarded flowers; see table 26.

[b] Respectively 72.2 and 37.3 per cent of the numbers of seeds planted.

smooth-leaved, approximates to 50 per cent, not 75 per cent, with little indication of selective elimination with poor germination.[16]

Here plainly, as with smooth-leaved, no pure mutant-type parent has yet been tested. Since this is also true of the other types, aside from early, that have been somewhat extensively tested, and fifty-three mutant-type parents in all have given Snowflake progeny, it is probable that homozygous individuals of these types seldom or never develop. The actual adult ratio with large-leaved is plainly not 2:1, but rather 1:1, a fact that would suggest absence of the mutant-type factor or factors from the pollen. The small trial cultures started in 1917, however, show that the type is carried by both sperm and eggs.

[16] Since hybrids are of the mutant type in appearance, the possible cross pollination by Snowflake parents could hardly give Snowflake progeny with any pure large-leaved parent. It may, however, have reduced slightly the proportion of large-leaved progeny from heterozygous parents of this type.

If we are dealing here with a type cytologically like *Oenothera gigas,* or rather the triploid *semigigas,* abnormal distributions of chromosomes may occur at meiosis, giving unpredictable genetic results. There has been special difficulty, as the numbers of doubtful individuals in table 26 suggest, in separating large-leaved from Snowflake, though in part of the cases the difference is extreme. Possibly some of the doubtful individuals are genetic intermediates due to irregular meiosis in triploid nuclei; such irregularities in division (Gates, 1915) occur with *Oenothera.* Both cytological examination and crosses with Snowflake are plainly required.

TABLE 28

Crenate-leaved type: numbers of apparent mutants and association of the type with singleness of flowers.

Culture	Progeny of Snowflake and early parents				
	Total examined[a]	Crenate-leaved			
		Single	Double	All	Coefficient of mutation
1908	725[b]	6	1	7	.97 ± .22
1910	338	3	0	3	.89 ± .32
1911F, seed house-sown	2072	13	3	16	.77 ± .13
All above	3135	22	4	26	.83 ± .11
All unselected	2410	16	3	19	.79 ± .12

[a] See note *b* to table 2.

[b] See note *c* to table 1.

4. THE CRENATE-LEAVED TYPE

This type (tables 1 and 3) is one of the three aberrant types of most frequent occurrence in the cultures here described, having constituted (table 28) about .79 per cent of the progeny of Snowflake and early parents. A large majority of the individuals have been singles, as table 28 shows. If the apparent mutants are produced by some process of segregation of factors, evidently the crenate and single factors were usually coupled in this material; if they are produced by immediate factor mutation, or are individually due to some change in a particular locus, evidently that locus is linked with the single-double locus and the change is more frequent in the single-carrying chromosomes; and finally, if they are due to reduplication or loss of a chromosome, the apparent linkage remains to be explained.

The margins of Snowflake leaves vary from entire or slightly sinuate to coarsely and irregularly dentate or serrate, this characteristic being subject to much environmental modification and varying

TABLE 29 [a]

Crenate-leaved type: heredity of apparent mutants and their descendants.

Parents	Progeny										
	Cultures	Seeds	Plants								
			Total examined		Crenate-leaved			Snowflake			Other types
			Undetermined	Determined	Single	Double	All	Single	Double	All	
22a	1911F & 1912	135, 28*, *107*	0	25	2	0	4	0	2	19 (20)	1
22b	1913	49	2	39	7	2	9	4 (5)	24 (25)	28 (30)	0
22c	1910 & 1911F	130, *111*	2	25	3	0	4	0	10	21	0
22d	1910 & 1911F	115	0	42	4	1	9	2	7	30 (31)	1 (2)
All P_1 crenate	All	429, 28*, *218*	4	131	16	3	26	6 (7)	43 (44)	98 (102)	2 (3)
22a–1	1913 & 1914	74	0	30	6	2	8 (9)	1 (2)	18	19 (20)	1
22a–5	1913	50	0	39	4	1	6	5	26	31	2
22c–1	1911H	20	0	18	3	2	5	3	9	12	1
22c–7	1911H	20	1	17	4	1	5	2	7	9	2 (3) [b]
22c–13	1911H	20	0	16	4	1 (2)	5 (6)	0	9	9	(1)
22d–8	1911H	20	0	18	3	1	4 (5)	3	8	11	2
22d–9	1911H	20	0	19	5	4	9	5	5	10	0
22d–12	1911H, 1913, 1914	168	4	109	20	13 (14)	33 (35)	8	57 (62)	65 (70)	4
22d–15	1911H, 1913, 1914	168	3	108	39	8	48	8	44 (46)	52 (54)	3 (6) [c]
All F_1 crenate	All	560	8	374	88	33 (35)	123 (128)	35 (36)	183 (190)	218 (226)	15 (20)

TABLE 29[a]—(*Continued*)

Crenate-leaved type: heredity of apparent mutants and their descendants.

Parents	Progeny										
	Cultures	Seeds	Plants								
			Total examined		Crenate-leaved			Snowflake			Other types
			Undetermined	Determined	Single	Double	All	Single	Double	All	
22c–7–7	1913	54	1	37	5	5	10	4	19 (21)	23 (25)	1 (2)
22d–12–8	1915–16	22	0	17	2	2	4	3	10	13	0
22d–15–13	1913	100	3	58	14	6	21	5	27 (28)	32 (33)	2 (4)
22d–15–28	1914	10	0	1	.....	.....	0	0	1	1	0
22d–15–32	1914	28	0	2	.....	.....	0	0	1 (2)	1 (2)	0
22d–15–66	1915–16	8	0	7	.....	.....	0	1	6	7	0
22d–15–98	1915–16	6	0	6	.....	.....	0	1	5	6	0
All F_2 crenate	All	228	4	128	21	13	35	14	69 (73)	83 (87)	3 (6)
All crenate	All	1217, 28*, *218*	16	633	125	49 (51)	184 (189)	55 (57)	295 (307)	399 (415)	20 (29)
22b–39	1914	48	0	4	.....	.....	0	(1)	1 (3)	1 (4)	0
22d–2	1911H	20	0	19	.....	.....	0	5	13	18	(1)
All Snowflake (2, F_1)	All	68	0	23	.....	.....	0	5 (6)	14 (16)	19 (22)	(1)

[a] See notes to table 24.

[b] The doubtful plant was suggestive of a combination of the crenate and narrow types.

[c] One of these doubtful plants perhaps crenate.

with the position of the leaves on the plant. In the crenate-leaved type this character is much accentuated, as can be seen by comparing figure 14 with figures 1 and 3; a warm greenhouse (fig. 14, upper line) gave very marked serration, while a cool greenhouse (lower plant, and also fig. 15) produced leaves much more nearly entire.

Under the much more extreme conditions of insolation, temperature, and humidity at Riverside, this type was often much dwarfed in comparison with Snowflake (figs. 16 and 17; see also fig. 23). In general, growth is weaker than with Snowflake and the stems more slender. Buds and flowers are often produced in great abundance, but the capsules are relatively few, small, and few-seeded. See tables 12 and 13 for internode data.

The progeny tests (table 29) show a slightly higher proportion of mutant-type progeny than occurred with smooth-leaved. A striking new feature appears for the first time in these results, the regular presence of linkage, or an association simulating linkage, with the single-double allelomorphs. Further, in all the four apparent mutants tested the crenate factor seems to be coupled with singleness, while among the sixteen F_1 and F_2 crenate parents there seem to be no crossovers.[17] We seem to be justified, for reasons just given, in summing the progeny as in the tables. Two things appear at once in table 29: (1) there is a great excess of total doubles over the usual 53 per cent; (2) there is a much greater excess of doubles with Snowflake than of singles with crenate; (3) the supposed double-recessive class (Snowflake double) is about two and one-half times as large as the double-dominant class (crenate single).

Table 30 adds two features of special interest. First, there is good evidence of selective elimination with poor germination; compare the remaining percentages with those for "Ithaca, field," "1915," "P_1," and "Germination poor," and see tables 39 and 40; the only exceptional case is the low percentage for the thirty plants of 1915–16. It would be surprising if the slow and weak growth of the crenate plants did not lead to such a result. Second, there is evidence that the crenate individuals are smaller than Snowflake even before germination. The seeds of crenate parents are less uniform in size than those of Snowflake parents; small seeds are numerous, and even the larger ones probably weigh decidedly less than normal Snowflake seeds. With five crenate parents included in the cultures of 1913, random

[17] With four of the parents the tests are obviously entirely inadequate; one other, 22d–9, gives no indication of linkage among nineteen progeny.

TABLE 30[a]

Crenate-leaved type: heredity. Summary.

Parents	Progeny					
	Cultures	Seeds	Plants			
			Total examined		Crenate	
			Undetermined	Determined	Number	Per cent
All crenate (10)	Ithaca, greenhouse	177, *7*	4	158	54 (56)	35.4 ± 2.5
All crenate (3)	Ithaca, field	343, *211*	0	59	7	11.9 ± 4.0
All erenate (10)	Ithaca, all	520, *218*	4	217	61 (63)	29.0 ± 2.1
All erenate (7)	1913	503	11	361	116 (118)	32.7 ± 1.6
All erenate (5)	1914	158	1	25	3 (4)	16.0 ± 6.2
All crenate (3)	1915–16	36	0	30	4	13.3 ± 5.6
All crenate (12)	Riverside, all	697	12	416	123 (126)	30.3 ± 1.5
All crenate (20)	All	1217, 28*, *218*	16	633	184 (189)	29.9 ± 1.2
All P_1 crenate (4)	All	429, 28*, *218*	4	131	26	19.8 ± 2.7
All F_1 crenate (9)	All	560	8	374	123 (128)	34.2 ± 1.6
All F_2 crenate (7)	All	228	4	128	35	27.3 ± 2.7
All erenate	Germination good	716, *7*	15	549[b]	174 (178)	32.4 ± 1.3
All crenate	Germination poor	501, 28*, *211*	1	84[b]	10 (11)	13.1 ± 3.4
All Snowflake (F_1, 2)	All	68	0	23	0	0

[a] See notes to table 24.

[b] Respectively 76.7 and 16.8 per cent of the numbers of seeds planted.

samples of seed were sorted, and the smaller and larger seeds planted separately.

Table 31 gives the data from this test. Here is practically conclusive evidence (see tables 39 and 40) that the smaller seeds much more often contain embryos of the crenate type.[18] Since the embryo of a *Matthiola* seed occupies practically all the space within the seed coats, it is evident that even as embryos Snowflake plants exceed

TABLE 31

Cultures of 1913. Crenate-leaved type: proportions from smaller and larger seeds of crenate parents.

Parent	Seeds		Progeny				
	Size	Number	Total determined	Crenate-leaved		Snowflake	Other types
				Number	Per cent		
22a–1	Smaller	21	6	4 (5)	83.3 ± 12.9	0	1
22a–1	Larger	29	23	3	13.0 ± 6.6	19 (20)	0
22a–5	Smaller	17	11	4	36.4 ± 9.5	6	1
22a–5	Larger	33	28	2	7.1 ± 6.0	25	1
22b	Smaller	13	8	5	62.5 ± 11.2	3	0
22b	Larger	36	31	4	12.9 ± 5.7	25 (27)	0
22d–12	Smaller	30	24	17	70.8 ± 6.5	5	2
22d–12	Larger	70	57	11 (12)	21.1 ± 4.2	42 (44)	1
22d–15	Smaller	32	24	17	70.8 ± 6.5	3	2 (4)
22d–15	Larger	68	54	18	33.3 ± 4.3	34 (35)	1
All	Smaller	113	73[a]	47 (48)	65.8 ± 3.7	17	6 (8)
All	Larger	236	193[a]	38 (39)	20.2 ± 2.3	145 (151)	3
All	All	349	266	85 (87)	32.7 ± 1.9	162 (168)	9 (11)

[a] Respectively 64.6 and 81.8 per cent of the numbers of seeds planted.

crenate plants in size. This fact, obviously, is further evidence in favor of the hypothesis of partial selective elimination of crenate heterozygotes during embryonic development.

It may be worth noting that the 73 plants from the smaller seeds include 6 (8) apparent mutants of other types (mutation coefficient 11.0 per cent), while the 193 plants from the larger seeds include only 3 apparent mutants (1.6 per cent).

Before we can profitably discuss these data further, we must consider the results from cross pollination (tables 32 and 33). The numbers, though small, make it very probable that both eggs and sperms carry the crenate factor. Further, it appears from series 20 that only a small portion of the sperms carry this factor, as we should expect from its apparent linkage with singleness. If homozygotes are nonviable, the combined crenate percentages of reciprocal crosses should

[18] The poorer germination of the smaller seeds suggests that the disparity between the two lots of seeds in the proportion of crenate embryos was even greater than the cultures indicate.

TABLE 32[a]

Hybridization of the Snowflake and crenate-leaved types; reciprocal crosses, F_1 generation.

Parents[b]	Progeny										
	Cultures	Seeds	Plants								
			Total examined		Crenate-leaved			Snowflake			Other types
			Undetermined	Determined	Single	Double	All	Single	Double	All	
20aa	1913	43	4	25	1	0	1	7 (8)	14	21 (22)	1 (2)
20bb	1913	76	1	64	4	(1)	4 (5)	22	32 (34)	54 (56)	3
20cb	1913	4	0	4	.....	.....	0	1	3	4	0
First three	1913	123	5	93	5	(1)	5 (6)	30 (31)	49 (51)	79 (82)	4 (5)
20dc, ed, & ic	1914	163	0	14	.....	.....	0	3 (4)	6 (10)	9 (14)	0
20de	1915–16	18	0	14	0	2	2	7	4	11	1
20ff	1915–16	50	0	45	1	0	1	17 (18)	22 (23)	39 (42)	1 (2)
20gf	1915–16	17	0	12	0	1	1	5	5	10 (11)	0
20gg	1915–16	15	0	14	1	0	1	5	7 (8)	12 (13)	0
20hd	1915–16	20	0	18	1	0	1	7	10	17	0
Last five	1915–16	120	0	103	3	3	6	41 (42)	48 (50)	89 (94)	2 (3)
All of series 20	All	406	5	210	8	3 (4)	11 (12)	74 (77)	103 (111)	177 (190)	6 (8)
21aa	1913	32	1	18	2	0	2 (3)	2	12 (13)	14 (15)	0
21bb	1914	34	0	1	.....	.....	0	0	1	1	0
21dd	1915–16	9	0	6	.....	.....	0	1	5	6	0
All of series 21	All	75	1	25	2	0	2 (3)	3	18 (19)	21 (22)	0
Snowflake parents of hybrids (5)	1913 & 1914	271.*50*	3	134	(1)	0	(1)	59 (63)	60 (64)	119 (127)	3

[a] See notes to table 24.

[b] Snowflake is the seed-parent type in series 20, and the pollen-parent type in series 21.

exeeed the pereentage from selfed parents; the expeeted high proportion with series 21, however, might well be realized with adequate numbers and good germination.

In spite of the small totals, it is very probable that linkage similar to that of the selfed eultures prevails with series 21. Where the erenate type is the pollen parent (series 20) linkage ratios are on our hypothesis impossible, sinee the eggs are all Snowflake and the sperms all double; the data, however, though statistieally inconelusive, suggest that the exeess of singles with erenate and of doubles with Snowflake is greatly redueed but not abolished.

TABLE 33

Hybridization of the Snowflake and crenate-leaved types. Summary.

Parents	Progeny					
	Cultures	Seeds	Plants			
			Total examined		Crenate	
			Undetermined	Determined	Number	Per cent
20aa, bb, & cb	1913	123	5	93	5 (6)	6.5 ± 1.6
20dc, ed, & ic	1914	163	0	14	0	0
20de,ff,gf,gg,&hd	1915–16	120	0	103	6	5.8 ± 1.5
All of series 20	All	406	5	210	11 (12)	5.7 ± 1.1
21aa, bb, & dd	All	75	1	25	2 (3)	12.0 ± 4.4
Snowflake parents of hybrids (5)	All	271, *50*	3	134	(1)	.7 ± .5

If we may ignore the doubtful correlation just mentioned a fairly adequate eomplete hypothesis for the selfing ratio is possible. Assume (1) a gametie ratio[19] of $5DC:1dC:1Dc:5dc$, or 16⅔ per eent of crossing over; (2) non-viability of homozygous erenate (CC); (3) low viability of simplex erenate (Cc), eliminating an average of 60 per cent of this type; and (4) eoupling of D and C in all parents tested. Evidenee has already been presented for assumptions (1), (2), and (3), exeept as to the intensity of linkage, while (4), as will be seen, is not at all improbable.

Random fertilization under these eonditions, exeepting (3), would give $26DdCc$ (erenate single) + $10ddCc$ (erenate double) + $5Ddcc$ (Snowflake single) + $25ddcc$ (Snowflake double). The other two classes, $5DdCC$ and $1ddCC$, would be non-viable pure erenate. Adding assumption (3) gives the following eomparison:

[19] Representing the singleness and doubleness factors by D and d, and the erenate factor and its "normal" allelomorph by C and c.

	DdCc	ddCc	Ddcc	ddcc
Theoretical ratio ($n = 44.4$)	10.4	4	5	25
Calculated for $n = 540$	126	49	61	304
Observed ($n = 540$)[20]	125	51	57	307

This fit surely cannot be criticised, whatever may be thought of the devices employed to obtain it! With cross pollination the agreement is fairly good in the case of series 20, which gives the only fairly reliable data. We are assuming $16\frac{2}{3}$ per cent of crossover dC sperms; elimination of .60 of $16\frac{2}{3}$ per cent, or 10 per cent of the total, gives $.06\frac{2}{3}/.90 = 7.4$ per cent expected crenate, as against 5.9 per cent observed. Series 21 is supposed to have 50 per cent of C eggs in the ratio $5DC:1dC$; elimination of .60 of this proportion, or 30 per cent of the total, would leave $.20/.70 = 28.6$ per cent, against 12.0 per cent in the very inadequate material observed. An adequate test of the hypothesis obviously requires large hybrid cultures, from vigorous seed sown under favorable conditions for germination.

A scarcity of crossover crenate singles follows from the hypothesis; they constitute only one twenty-sixth of the total number of viable crenate single progeny of crenate parents. No direct evidence indicating that the crenate and double factors are ever coupled in singles has yet been discovered.

If the supposed crenate mutants are due to immediate factor mutation, however, it seems strange that the same locus is changed more readily in a singleness chromosome than in one carrying the doubleness factor, in a ratio similar to the linkage ratio of later generations. If the apparent mutants are really segregates from a balanced-lethal combination, the observed original coupling of crenate with single might be an accident of sampling involved in the original choice of material; other initial parents might give the reverse coupling.

5. THE SLENDER TYPE

This type is comparatively rare as an apparent mutant from Snowflake or early; the 3135 plants reported in table 28 gave only 4 (6) mutants (2 singles and 4 doubles, 2 of the latter perhaps Snowflake), a mutation coefficient not over .19 per cent. This type seems to occur more frequently among progeny of crenate, a type similar in some

[20] Omitting 29 plants classed as neither crenate nor Snowflake, which as probably non-crenate should perhaps be added to Snowflake, and also 64 plants (13 crenate and 51 Snowflake) with flower data incomplete. Complete data for the total of 633 plants would plainly give a somewhat poorer fit, but this could be improved by assuming a slightly greater elimination of *Ccii* zygotes.

TABLE 34[a]

Slender type: heredity of apparent mutants and their descendants.

Parents	Progeny										
	Cultures	Seeds	Plants								
			Total examined		Slender			Snowflake			Other types
			Undetermined	Determined	Single	Double	All	Single	Double	All	
25a	1913	*19*	1	1	(1)	0	(1)	.....	.....	0	0
25b	1910, 1911F, & 1913	173, *21*	0	83	9[b] (11)	8 (9)	17 (20)	1	58 (62)	59 (63)	0
All P_1 slender	All	192, *40*	1	84	9 (12)	8 (9)	17 (21)	1	58 (62)	59 (63)	0
25b–6	1911H, 1913, 1914	94	0	56	10	4	14	2 (3)	32 (37)	35 (41)	1
25b-9	1911H	20	0	20	0	1	1	0	17	17	(2)
25b–11[c]	1911H & 1913	70	1	31	4	11 (15)	16 (21)	0	8	8	1 (2)
25b–79	1914	39	0	1	.....	.....	0	0	1	1	0
All F_1 slender	All	223	1	108	14	16 (20)	31 (36)	2 (3)	58 (63)	61 (67)	2 (5)
25b–6–8[c]	1913	*42*	0	7	2	1	3	0	4	4	0
25b–6–8–6	1915–16	53	0	44	15 (16)	2	18 (19)	1	24	25	0
All slender	All	510, *82*	2	243	40 (44)	27 (32)	69 (79)	4 (5)	144 (153)	149 (159)	2 (5)
All "extreme" slender	All	112, *42*	1	38	6	12 (16)	19 (24)	0	12	12	1 (2)
All "ordinary" slender	All	398, *40*	1	205	34 (38)	15 (16)	50 (55)	4 (5)	132 (141)	137 (147)	1 (3)

[a] See notes to table 24.

[b] One of these "apparently" single.

[c] Described as "extreme" specimens of the slender type.

respects, and *vice versa*. Under favorable conditions this type may closely resemble Snowflake, but is decidedly more slender in stems, leaves, and pedicels. A characteristic drooping of flowers and branches is well shown by two plants in figure 18; the single is 25b of the tables. The progeny of 25b shown in figure 19 illustrate a variability of the "slender" characteristics which has suggested the presence of genetic differences among plants classed as slender. The leaves often resemble those of crenate more closely than do Snowflake leaves.

In the field at Ithaca flowering was markedly earlier than with Snowflake, and the type seems to be earlier on the whole. The Riverside conditions have commonly given a decided dwarfing as compared with Snowflake, though not to the extreme degree that this has occurred with crenate (figs. 20 and 21).

The results of selfing tests are reported in tables 34 and 35. The distributions have the same general characteristics as with crenate, with some remarkable differences. The excess of doubles with Snowflake is very much greater, the ratio being about 30:1; with slender, however, the excess of singles is slight in the grand total and perhaps significantly variable with different parents.

Plant 25b–11, the "extreme" individual of figure 19, appears to give a real excess of slender over Snowflake, and of double slender over single slender, though the numbers are much too small for certainty. The two parents classed as "extreme" are (tables 39 and 40)[21] quite probably genetically different from the other slender parents. It should be noted that plant 25b–6–8–6, progeny of one of the parents described as "extreme," has also given a relatively high proportion of slender progeny. Perhaps the "extreme" form is heterozygous for a second slenderness factor similar to the original one.

The percentages of mutant-type progeny are (table 39) much more variable than with smooth, large, or crenate, and (table 40) there is no good evidence of selective elimination; both these facts may depend on genetic differences among the parents tested.

The great modifiability of the various types, including Snowflake, indicated by a comparison of, for instance, figures 14, 15, and 16, greatly complicates the positive determination of types. In the cultures of 1911H and 1913, where crowing in flats or aphis injury in the field interfered with normal development of some plants, the impression was obtained that the slender type occurred in several grades

[21] In the calculation of the probability of simple sampling, f is taken as 3 (the number of cultures), not 2 (the number of parents).

TABLE 35

Slender type: heredity. Summary.

Parents	Progeny					
	Cultures	Seeds	Plants			
			Total examined		Slender	
			Undetermined	Determined	Number	Per cent
All slender (4)	Ithaca, greenhouse	75	1	71	14 (18)	25.4 ± 3.7
All slender (1)	Ithaca, field	137	0	51	8	15.7 ± 4.4
All slender (4)	Ithaca, all	212	1	122	22 (26)	21.3 ± 2.9
All slender (5)	1913	182, *82*	1	73	29 (34)	46.6 ± 3.7
All slender (2)	1914	63	0	4	0	0
All slender (1)	1915–16	53	0	44	18 (19)	43.2 ± 4.8
All slender (7)	Riverside, all	298, *82*	1	121	47 (53)	43.8 ± 2.9
All slender (8)	All	510, *82*	2	243	69 (79)	32.5 ± 2.0
All P_1 slender (2)	All	192, *40*	1	84	17 (21)	25.0 ± 3.4
All F_1 slender (4)	All	223	1	108	31 (36)	33.3 ± 3.0
All F_2 and F_3 slender (2)	All	95, *42*	0	51	21 (22)	43.1 ± 4.4
All slender	Germination good	199, *21*	1	165[a]	47 (55)	33.3 ± 2.5
All slender	Germination poor	311, *61*	1	78[a]	22 (24)	30.8 ± 3.6
"Extreme" slender (2)	All	112, *42*	1	38	19 (24)	63.2 ± 5.1
"Ordinary" slender (6)	All	398, *40*	1	205	50 (55)	26.8 ± 2.2

[a] Respectively 82.9 and 25.1 per cent of the numbers of seeds planted.

probably unlike genetically. In the 1916 cultures, on the other hand, with better development, this type seemed substantially as uniform as the others.

If we ignore these possible genetic differences and attempt to apply the scheme worked out for crenate, difficulties appear at once. First, the scarcity of Snowflake singles would indicate much closer linkage than with crenate, while the relative abundance of slender doubles apparently contradicts this supposition. Second, the inadequate results from crossing with Snowflake (table 36) suggest that the sperms carry the supposedly crossover slender factor at least as often as do the eggs. While crenate as pollen parent gives results agreeing tolerably with the hypothesis, slender gives results differing from these in the wrong direction.

No doubt, however, the disagreements can be over emphasized. Both crenate and slender as seed parent seem to give the expected relations between singles and doubles, and series 23 also does this with the Snowflake progeny. Obviously the functional sperms and eggs of these mutant-type parents exhibit different ratios between types, and the peculiar results in other respects with slender may be related to the added complication suggested above. The astonishing feature of the data, of course, is the great excess of single slender over double slender in series 23—an excess which suggests an actual significant excess of singles in the totals of all types given by this cross—while with selfed slender there is a great total deficiency of singles. We may at least feel confident that the modifications of the single-double ratio, with this type and with crenate, are due to lethal action which also affects the proportions of viable slender and crenate gametes or zygotes.

If differential viability before germination is an important factor with these types, very probably it differs according as Snowflake or the mutant type is the seed parent, and according to the parental environment. In other words, partial selective elimination during seed formation may vary with the environment of the embryos, according as this environment is affected by either the genetic constitution or the external environment of the seed parent. Until such uncertainties are eliminated, we are hardly justified in ruling out, for the types discussed, the probability that regular segregation and (in the last two cases) true linkage are concerned in these phenomena. In fact, the definite differences in ratios between reciprocal crosses and between at least one of the crosses and selfing encourage further attempts at satisfactory factorial analysis.

TABLE 36

Hybridization of Snowflake and slender; reciprocal crosses, F_1 generation.

Parents[a]	Progeny											
	Cultures	Seeds	Plants									
			Total examined		Slender				Snowflake			Other types
			Undetermined	Determined	Single	Double	All		Single	Double	All	
							Number	Per cent of total				
23aa, bb, & cc	1914	114	1	6	....	.....	0	0	1	1 (5)	2 (6)	0
23ca	1915–16	25	0	23	4	1	5	21.7 ± 5.8	6	10	16	2
23ea	1915–16	120	0	93	20	(1)	20 (21)	22.6 ± 2.9	32 (33)	33 (35)	65 (68)[b]	2 (4)
All of series 23	All	259	1	122	24	1 (2)	25 (26)	21.3 ± 2.5	39 (40)	44 (50)	83 (90)	4 (6)
24aa	1915–16	53	0	21	2	0	2	9.5 ± 4.3	0	18	18	1
Series 23 and 24	Germination poor	167	1	27[c]	2	0	2	7.4 ± 3.4	1	19 (23)	20 (24)	1

[a] Snowflake is seed parent in series 23, and pollen parent in series 24.

[b] These three doubtful plants had leaves alone resembling slender, evidently because of ill health; one, recovering after pruning, lost its slender appearance. The doubtful slender double very probably also belongs here.

[c] 16.2 per cent of the number of seeds planted.

6. THE NARROW-LEAVED TYPE

As table 37 indicates, this type competes with crenate for second place in frequency of occurrence in the Ithaca cultures; in fact, when only the strictly unselected cultures are considered the percentage is very close to that for smooth-leaved. A feature of special interest is the apparent association of the mutant type with doubleness.

In a cool greenhouse this type (fig. 22) varied from exceptionally late and many-noded to ordinary in both characters. The leaves (see also fig. 18) were typically narrow, rather strictly entire, often rolled backward or twisted, and typically more ascending than those of

TABLE 37

Narrow-leaved type. Numbers of apparent mutants and association of the type with doubleness of flowers.

Culture	Progeny of Snowflake and early parents				
	Total examined[a]	Narrow-leaved			
		Single	Double	All	Coefficient of mutation
1908	725[b]	0	2	2	.28 ± .26
1910	338	1	4	6	1.78 ± .38
1911F, house-sown	2072	7	12	20	.97 ± .15
All above	3135	8	18	28	.89 ± .12
All unselected	2410	8	16	26	1.08 ± .14

[a] See note *b* to table 2.

[b] See note *e* to table 1.

Snowflake. The apex of the leaf is often more acute than with Snowflake, and many leaves are mucronate or at least end in a sharp, rigid tip.

A striking characteristic is the narrowness of the sepals, resulting in frequent early separation at the edges, partially exposing the petals in immature buds.

Under the less favorable field conditions the plants often remain long as dwarf rosettes, and flower late and feebly if at all. Figures 23 and 24 show comparatively well developed plants in the field.

The type is on the whole very distinct in the field, though there has been some question whether a greenhouse plant such as that in figure 18 is genetically different from those with short and rigid leaves (figs. 22 and 24); the very great variability in leaf form due to external conditions makes such a question very difficult without extensive progeny tests. It is now (1918) probable that narrow-dark (p. 143) was not distinguished from narrow in the greenhouse.

TABLE 38[a]

Miscellaneous mutant types: heredity of apparent mutants.

Parents	Cultures	Seeds[a]	Progeny									
			Plants									
			Total examined		Parental type				Snowflake			Other types
			Undetermined	Determined	Single	Double	All		Single	Double	All	
							Number	Per cent of total				
33a	1911H & 1913	41	0	22	0	1	1	.....	8 (10)	8 (10)	16 (20)	1[c]
33b	1913	45	0	15	1	2	3	....	5 (6)	6	11 (12)	1
All narrow-leaved	All	86, *45*	0	37	1	3	4	10.8 ± 3.4	13 (16)	14 (16)	27 (32)	2
"Short stout" (1, P_1)	1911H & 1913	39	0	29	0	3 (5)[b]?	5 (7) ?	24.1 ± 5.4?	10 (11)	11	21 (22)	0
27a, "small convex-leaved?"	1913 & 1914	98	5	44	1?	1?	2 (4)?	9.1 ± 2.9?	9 (12)	16 (18)	25 (30)	3 (5)

[a] See note *b* to table 24.

[b] One of these "evidently" double.

[c] Narrow-dark-leaved type.

The few singles have produced few seeds, and these were highly variable in size. The capsule often has a defective septum, more or less of the distal portion being absent. Germination was poor in the small cultures secured (table 38, upper part), with only 10.8 per cent of the mutant type among the progeny.

This case agrees in most respects with those previously discussed, but adds one point of interest in the occurrence of apparent coupling of mutant type with doubleness rather than singleness. Seed appears to be less abundant and less well developed than with any of the preceding mutant types, facts probably significant in relation to the low percentage of narrow progeny from narrow parents, though the large probable error of the percentage must be considered.

7. MISCELLANEOUS ABERRANT TYPES

As part of the aberrant individuals occurring in the greenhouse were either doubles or singles that produced no seed, while practically no seed was produced by any plants in the field at Ithaca or by even some of the commoner mutant types at Riverside, the opportunity for progeny tests has been almost entirely limited to the types so far discussed.

The narrow-dark-leaved type (table 3) was common and distinct in the field at Ithaca, where it constituted about .48 per cent of the 2072 plants from house-sown seed, and has been readily identified in several cases at Riverside. It was not distinguished in the greenhouse cultures, but was very probably included under narrow-leaved. Possibly a single described as "small-convex-leaved" belonged to this type, though two field plants were given this name as distinct from narrow-dark; according to a photograph (fig. 25, second plant from left), another greenhouse plant (a double) may have been similar to narrow-dark-leaved. The narrow-dark-leaved type (figs. 26 and 27) has narrow dark-green leaves, strongly convex upward, and evidently tends to compactness of growth and lateness of flowering; under field conditions it seems decidedly more like Snowflake than like narrow-leaved.

The 44 progeny (table 38) secured from the greenhouse single mentionad above included 2 (4) narrow-dark-leaved individuals and 3 (5) other plants not Snowflake (the last including two smooth, one large, one slender, and one semicrenate), besides five undetermined plants. Plainly the type of the parent is still in doubt.

Another very different greenhouse plant, described as "stout dwarf" (fig. 25, third from left), gave among 29 progeny (table 38) 5 (7) individuals evidently not Snowflake, which may have been narrow-dark or may have belonged to another type that was somewhat similar under the conditions of the tests. The parent resembled Snowflake except in its short internodes and short, stout capsules.

Four other plants suspected of mutation apparently entirely failed to repeat their type in their progeny, perhaps because of the smallness of the house cultures. One of these was the plant, much branched for the warm greenhouse, third from the right in figure 18; another was a very late plant with a remarkably large number of main-stem leaves; the others were a plant with unusually small flowers and one with some of the leaves somewhat spatulate. Possibly all of these were Snowflake, though the second, which gave poor germination, probably was not. All these four plants have been included as Snowflake parents for tables showing numbers of apparent mutants.

The small-smooth-leaved type is well shown in figure 25 (first and fifth from the left). It is the smallest and weakest of the fairly common and definitely identified types; it has small, very smooth leaves, and is late in blooming. The two plants shown were both singles, but they set no seed.

The semicrenate-leaved type (table 3) differed slightly but apparently definitely from Snowflake, somewhat resembling crenate-leaved in leaf form. The one "pointed-crenate-leaved" plant of table 3 may have been crenate-leaved. The "compact" and "curly-leaved" plants of this table have not been identified with any aberrant types in other cultures. With the remaining six types of table 3 all the individuals have been questioned as possibly Snowflake; it is now practically certain that some of those in the second, third, and fourth groups belonged to the large-leaved type since studied, but the apparent intergradation with Snowflake makes any attempt at a definite reclassification from the records a matter of doubtful value.

The second plant from the right in figure 25 was remarkable for its short stem and few but large leaves. Several other more or less exceptional individuals have appeared in the cultures, especially among some plants with abnormal cotyledons, selected from large numbers of greenhouse seedlings in the 1908 cultures, which were examined for syncotyledony. Some of these were very weak plants which finally died without flowering.

The fluctuations in habit, leaf form, etc., within the type are such that the determination of familiar types is often a matter of some uncertainty, as is shown by data that have been presented. It may well be that among the doubtful types are included several definite but comparative rare mutant forms, which occurred too infrequently to afford adequate material for positive classification.

8. SOME PROBABILITES OF RANDOM SAMPLING

For compactness of presentation and convenience of comparison the material in tables 39 and 40, to which some incidental references have already been made, is collected here rather than scattered through the disenssions of the various types concerned. Some statements as to methods are also necessary in connection with each of the topics here treated.

First, it should be noted that the percentages previously given have regularly been accompanied by the probable errors of simple sampling. These probable errors have been calculated by the formula $E_{\text{per cent}} = .6744898\sqrt{\frac{pq}{n}}$, where p is the percentage of the mutant type ("successes"), q is $1 - p$, and n is the size of the sample (the number of plants concerned).

In the heredity tables for each type, p has uniformly been taken as the percentage of the total of the lots compared, or p_0.

For the "mutation coefficient" the percentage of the grand total of unselected house-sown lots has regularly been used. Evidently the few selected progeny included in tables 1, 28, and 37 should be omitted. All the percentages here are so low that the probable errors deserve little confidence, even though n is usually fairly large. The rather close agreement of the percentages of all apparent mutants in the three distinct lots of unselected house-sown cultures suggests that they represent fairly well the population value for the potentialities of the seeds; and even if the mean percentage of the total of the lots for the main comparisons is actually nearer, it is safer to use the larger probable errors resulting from the method here employed. Furthermore strict use of p_0 would sometimes require several slightly different probable errors for the same percentage, for use in different comparisons in the same table.

If the probable error of the difference of any two percentages in the same table is to be obtained, therefore, formulae corresponding to those given by Yule (1911, pp. 264–267) are applieable.

Now, it is possible in some of these cases to calculate the aetual standard deviation of the percentage in subsamples which make up an aggregate sample. Table 39 gives sueh aetual standard deviations, in comparison with the eorresponding theoretical or expeeted standard deviations given by

$$\sigma_{\text{per cent}} = \sqrt{\frac{pq}{\bar{n} - 3}}.$$

TABLE 39

Standard deviations of percentages of mutant types. Values derived from $\sqrt{pq}$, *compared with values expressing the actual variability of subsamples.*

Type of parent and grouping of progeny	N	f	$\bar{n}$	p	Standard deviation of samples of mean size $\bar{n}$		
					Actual	Theoretical, $\sqrt{\frac{pq}{n-3}}$	Difference / $E\sigma$
Smooth-leaved type:							
All lots by parentage	234	6	39.0	27.35	7.5	7.4 ± 1.4	+ .1
All lots as grown	234	12	19.5	27.35	11.3	11.0 ± 1.5	+ .2
Germination good	187	7	26.7	29.95	10.9	9.4 ± 1.7 9.2[a]	+ .9
Germination poor	47	5	9.4	17.02	5.2	14.9 ± 3.2 17.6	− 3.0
Large-leaved type:							
All lots by parentage	357	20	17.85	49.02	10.7	13.0 ± 1.4	− 1.6
All lots as grown	357	22	16.2	49.02	10.9	13.7 ± 1.4	− 2.0
Germination good	260	14	18.6	50.38	11.3	12.7 ± 1.6 12.7	− .9
Germination poor	97	8	12.1	45.36	8.7	16.5 ± 2.8 16.6	− 2.8
Crenate-leaved type:							
All lots by parentage	633	20	31.65	29.86	10.6	8.6 ± .9	+ 2.2
All lots as grown	633	28	22.6	29.86	12.5	10.3 ± .9	+ 2.4
Germination good	549	20	27.45	32.42	10.7	9.5 ± 1.0 9.3	+ 1.2
Germination poor	84	8	10.5	13.10	10.5	12.3 ± 2.1 16.7	− .9
Seed-size test, smaller seeds	73	5	14.6	65.75	13.2	13.9 ± 3.0 13.8	− .2
Same, larger seeds	193	5	38.6	20.21	9.4	6.7 ± 1.4 7.9	+ 1.9
Same, all seeds, by parentage	266	5	53.2	32.71	10.3	6.6 ± 1.4	+ 2.6
Same, all seeds, as grown	266	10	26.6	32.71	22.9	9.7 ± 1.5	+ 8.8
Slender type:							
All lots by parentage	243	8	30.4	32.51	17.5	9.0 ± 1.5	+ 5.7
All lots as grown	243	13	18.7	32.51	19.7	11.8 ± 1.6	+ 4.9
Germination good	165	7	23.6	33.33	14.9	10.4 ± 1.9 10.3	+ 2.4
Germination poor	78	6	13 0	30.77	27.2	14.6 ± 2.8 14.8	+ 4.5
Parents "extreme"	38	3	12 7	63.16	14.4	15.5 ± 4.3 15.1	− .3
Parents "ordinary"	205	10	20.5	26.83	14.7	10.6 ± 1.6 11.2	+ 2.6
Narrow-leaved type:							
All lots as grown	37	3	12.3	10.81	8.1	10.2 ± 2.8	− .75

[a] The second values for some cases in this column are derived from p_0 (see text).

For example, table 27 gives the percentage of large-leaved plants among the 357 progeny of the 20 large-leaved parents as 49.0 ± 1.8 per cent. This probable error is given by $.6744898\sqrt{\frac{pq}{n}}$, where $p = 49.0$ per cent, $q = 51.0$ per cent, and $n = 357$. These 357 progeny, as table 39 indicates, came from 20 parents which contributed an average of 17.85 progeny each, and the actual standard deviation of the percentage in these 20 sibships was 10.7 per cent.

Obviously the expected standard deviation of simple sampling for comparison must represent samples not of 357 plants each but of 17.85 plants each. Now a percentage is obviously a mean (of values all either 0 or 1). Since "Student" (1908) has shown that the theoretical standard deviation of the mean in samples is given more exactly by

$$\sigma_{\text{mean}} = \frac{\sigma_{\text{variate}}}{\sqrt{n-3}} \text{ than by } \sigma_{\text{mean}} = \frac{\sigma_{\text{variate}}}{\sqrt{n}}$$

(the value for the normal curve conventionally used for the probable error of the mean) and since $\bar{n}$, the mean size of sample, is small enough to make the correction a matter of considerable importance, $\sqrt{\bar{n}-3}$ is here used. Since $\sigma_{\text{variate}} = \sqrt{pq}$, we have $\sigma_{\text{mean}} = \sqrt{\frac{pq}{\bar{n}-3}}$, where $\bar{n} = 17.85$. This gives a theoretical standard deviation of 13.0 per cent.[22]

It is true (Yule, 1911, p. 260) that the ordinary method of calculation of the actual standard deviation is not satisfactory for means when the samples vary in size. A method has been used, however, which obviates this difficulty, so that comparison with the results given by $\sqrt{\frac{pq}{\bar{n}-3}}$ is strictly legitimate. Each squared percentage deviation has been weighted by multiplying it by the number of individual plants which it represents, and the summation of squared deviations has then been divided, not by Σf, the number of samples, but by $\Sigma f \times \bar{n}$, the number of samples multiplied by the mean weight or average size of sample (in other words, by N, the total number of individuals).[23]

[22] In the calculations for table 39 p has been taken as the percentage given in this table, to two decimal places, while with all other numbers employed in calculation, including $\bar{n} - 3$, three or more decimal places have been used as needed.

[23] Algebraic proof of the correctness of the method has kindly been furnished by Frank L. Griffin, Professor of Mathematics, Reed College, Portland, Oregon. If it develops that this rather obvious device has not been suggested for the purpose, it is to be presented elsewhere with the mathematical proof. When the variates are not grouped in classes the calculation is substantially as easy as without weighting, while the theoretical value is found with much less work than by the method given by Yule (1911, p. 260), which requires the harmonic mean of the sample sizes.

TABLE 40

The probability of certain differences of percentages of mutant types considered as deviations of simple sampling.

Problem	Probability			
	Assuming one population. (zero as most probable true difference)		Assuming two populations (sample difference most probable true difference)	
	Chance of deviation	Odds against deviation	Chance of deviation	Odds against deviation
Good vs. poor germination:				
With smooth type	.2646	2.8 : 1	.1083	8.2 : 1
With large type	.5466	.8 : 1	.2724	2.7 : 1
Same, $f_o = \sqrt{f_1 f_2}$	.4910	1.0 : 1	.2445	3.1 : 1
With crenate type	.0320	30.25 : 1	.0066	150.5 : 1
Same, $f_o = \sqrt{f_1 f_2}$	.0064	155.25 : 1	.0008	1249.0 : 1
With slender type	.7682	.3 : 1	.3835	1.6 : 1
With all types	.....	.....	.000074670	13,391 : 1
Same, $f_o = \sqrt{f_1 f_2}$[a]	.....	.....	.0000081239	123,093 : 1
Small vs. large seeds:				
With crenate type	.0046	216 : 1	.0020[b]	499 : 1[b]
"Extreme" vs. "ordinary" parents:				
With slender type	.1114	8.0 : 1	.0557	17.0 : 1
Same, $f_o = \sqrt{f_1 f_2}$	.0180	54.6 : 1	.0090	110.1 : 1

[a] That is, using for large and crenate the values given by this formula (see text).

[b] If the actual standard deviation of the five differences is used, $P = .0006$ and the odds are 1666:1 (see text).

In the calculation the deviations are taken from zero, and with these small numbers of samples the percentages are not thrown into classes; it suffices, then, to square each number of "successes," divide by the corresponding total of individuals, add the quotients, and divide by the grand total of individuals, correcting this weighted mean squared deviation by subtracting the square of the weighted mean percentage (percentage of grand total). If s is the number of successes and n is the total number of individuals in the subsample, and M is the weighted mean percentage, then $M = \frac{\Sigma s}{\Sigma n}$, and

$$\sigma_{\text{per cent}} = \sqrt{\frac{\sum \frac{s^2}{n}}{\Sigma n} - M^2}.$$

Table 39 gives, for the most important comparisons of heredity percentages, the total number of progeny (N), the number of cultural groups or (with the first line for each type) the number of parents (f), the average size of the groups of progeny ($\bar{n}$), and the mean percentage of the mutant type (p). This serves as a summary of some of the most important statistical data already presented relating to the inheritance of these types, and also shows the basis of the remaining part of this table and of table 40. For comparison of actual and theoretical standard deviations the theoretical value has been calculated from the actual percentage as given in this table. For comparison of means (table 40) the percentage of the corresponding total (p_0) has also been used, this theoretical standard deviation being the second in the table in the cases where the two values are not identical.

Since small changes in a percentage have little effect on its theoretical standard deviation, we are fairly well justified in taking the latter, as calculated from the actual percentage in each case, to be the "population" value. Consequently, the difference between the theoretical and actual standard deviations has been expressed in each case as a multiple of the probable error of the theoretical value.

Aside from the last line for crenate-leaved, where there is an obvious artificial reason for high variability, there is no very significant difference except with slender. In this case, the deviation of 5.7 times the probable error (line 1) is probably largely due to the genetic differentiation of "extreme" and "ordinary" parents suggested by their appearance and by the wide difference in the heredity percentages; the differences become moderate when the progeny of the two classes of parents are separated.

In the two cases (smooth-leaved and crenate-leaved types) where the percentages of mutant types differ greatly with good and poor germination, separation according to germination gives a mean value of the standard deviation decidedly lower than the value for all lots taken together. In the case of the large-leaved type there is little change, while the considerable reduction with the slender type is probably due to unequal separation of lots from parents genetically different.

Table 40 shows the simple-sampling probability of the most striking differences of heredity percentages, aside from the characteristic differences between different types. "Student's" (1917) table of probabilities of mean deviations with small samples is used, with interpolation by second differences. Where the standard deviation of the difference is required it is found from the theoretical values given in table 39 by the formula (Yule, 1911, pp. 264–265)

$$\sigma_{\text{difference}} = \sqrt{\sigma_1 + \sigma_2} = \sqrt{\frac{p_0 q_0}{n_1 - 3} + \frac{p_0 q_0}{n_2 - 3}},$$

when one statistical population is assumed (table 40, columns 2 and 3). When two populations are assumed (table 40, columns 4 and 5) the corresponding formula using p_1q_1 and p_2q_2 is employed. In the one case where this is possible (the seed-size test), it is also calculated from the actual differences of the pairs of percentages in the separate tests, each difference being weighted with the total number of progeny from the parent concerned. Where two values of f (the n of "Student's" table) are involved, the smaller is taken, giving understatements of the probabilities involved; in the two cases where the difference is more than 2, the values are recalculated, with f as the nearest smaller integer to the geometric mean of the two actual numbers (that is with $f_0 = \sqrt{f_1 f_2}$). In the case where the probabilities of four deviations all in the same direction are combined, the four chances of occurrence are multiplied together; that is, if the $\frac{1}{2}(1 + a)$ of "Student's" table is P, and $1 - P$ is F, then $F_{1\cdot2\cdot3\cdot4} = F_1 \cdot F_2 \cdot F_3 \cdot F_4$.

"Student" (1908, p. 1) says, "The usual method of determining the probability that the mean of the population lies within a given distance of the mean of the sample, is to assume a normal distribution about the mean of the sample . . . ." When this is done with a difference of means, it is at once evident that only half of the chances of deviations as great as the distance of the given difference from zero difference lie below zero difference; the other half of the chances of

such deviations lie in the opposite direction and represent positive differences still greater than the sample difference. In other words, if the implications of a sample difference are to be given full weight, this difference must be considered the *most probable value* of the theoretical "true" difference between *two assumed distinct statistical* populations. In the present case we wish to know the probability that the "true" or theoretical-population means differ in the same sense as the observed sample means. This involves calculation of the probability of deviations in one direction (beyond zero difference) from the sample difference. If the sample difference of means is considered as positive, then the negative "tail" of the theoretical frequency curve of sample differences (this curve being centered at the observed sample difference) must be compared with the rest of the curve. The positive portion of the curve the $\frac{1}{2}(1+\alpha)$[24] of the tables, then gives the chances favoring the hypothesis that the sample means truly represent the population means. The odds in favor of the hypothesis are therefore given by the formula

$$0_1 = \frac{\frac{1}{2}(1+\alpha)}{\frac{1}{2}(1-\alpha)} \text{ or } \frac{\frac{1}{2}+\frac{1}{2}\alpha}{\frac{1}{2}-\frac{1}{2}\alpha}.$$

Values calculated from this formula are given in columns 4 and 5 of table 40.

When other considerations than the sample evidence are to be taken as determining the most probable value of the "true" mean, the case is different. For example, if the probability that our sample percentages are mere sampling deviations from some theoretical Mendelian value were in question, that theoretical value must be taken as the population mean and only the magnitude of the deviations must be considered.

When a difference of means is considered from this latter standpoint, it is assumed that the two samples come from *one statistical population*, and hence that zero is the most probable value of the population difference. If we choose to assume that the most probable value of the population difference in our cases is zero, we must calculate the odds against a deviation of the observed amount in either direction from zero difference. The formula for these odds is

$$0_2 = \frac{\frac{1}{2}(1+\alpha)-\frac{1}{2}(1-\alpha)}{2\times\frac{1}{2}(1-\alpha)} \text{ or } \frac{\alpha}{1-\alpha}.$$

[24] The whole area of the frequency curve is taken as unity, and α is the area enclosed by any given deviation in both directions from the mean.

Values from this formula are given in columns 2 and 3 of table 40; their magnitude in three cases, however, and the uniform agreement of the direction of difference with the expectation from biological evidence which has been discussed, weigh heavily in each test against the assumption of random sampling from a single statistical population.

It does not appear necessary, however, thus to weigh the evidence in detail before deciding which formula is suited to the case. There is no evident theoretical value from which these percentages are reasonably likely to be *sampling* deviations. This being the case, and granting such general possibilities as that of differential viability, it seems most reasonable to use the former (0_1) formula. That is, we should give full weight to the implications of a sample deviation unless there is some definite reason for assuming that some other value better represents the mean of the theoretical statistical population.

It must be remembered that the actual probabilities of sampling deviations do not necessarily correspond closely with the probabilities of *random* sampling. With the material in table 40, however, aside from the germination comparison in the case of the slender type, table 39 suggests a fair agreement with the conditions of random sampling. The actual standard deviations of the subsamples do not in general differ widely from the corresponding theoretical values, and the differences are negative about as often as positive.

The hypothesis of selective elimination with poor germination is strongly sustained (table 40), although only one difference (with the crenate type) has much statistical significance when considered alone. If we may multiply together the members of the four ratios in column 3 of the table, the combined odds (using the f_0 values) are 130:1 against occurrence of these four deviations as accidents of simple sampling, when magnitude of deviation alone is considered. If direction of deviation alone is considered the random chance of these four deviations all in the same direction is obviously $(\frac{1}{2})^4$, or the odds favoring the elimination hypothesis are 15:1. Combination of these two chances indicates a high probability for the hypothesis. When the two-population formula is used in calculating the standard deviation of the difference (columns 4 and 5) the value of P is considerably reduced in some cases, and the combined odds obtained from $F_1 \cdot F_2 \cdot F_3 \cdot F_4$ are very high. Evidently the best single expression of the simple-sampling odds, though possibly somewhat too high, is the value given last in column 5, or 123,093:1.

With the seed-size test of crenate the odds are 499:1 with the theoretical standard deviation of the difference, or 1666:1 with the

actual standard deviation. When the relatively small size and weak growth of crenate seedlings are also taken into account, the relatively small average size of crenate embryos may be considered to be demonstrated beyond reasonable doubt.

With "extreme" and "ordinary" slender parents the odds decidedly favor the hypothesis of genetic differentiation of parents, in spite of the small numbers involved. We must remember that definite statistical differentiation of lots of progeny grown under uniform conditions does not necessarily demonstrate *genetic* differences (differences in output of gametes) between the parents; in this case, however, the difference in the appearance of the parents and in the single-double ratio among the progeny also suggest genetic differentiation.

GENERAL DISCUSSION[25]

It might be argued with some plausibility that the available evidence hardly justifies conventional factorial analysis, or at least that the data indicate strongly the presence of marked factorial inconstancy. The aberrant types occur in very small proportions among the progeny of selfed Snowflake parents, in much larger proportions from "mutant-type" parents, and in intermediate proportions from crosses with Snowflake. It might be supposed that the Snowflake type has a slight tendency to mutate to the other types, and that these have a much more marked tendency to mutate back to Snowflake. Various considerations, however, especially the occurrence of apparently regular linkage phenomena, seem to favor the general form of hypothesis which has been presented.

As we have seen, it is well known from the behavior of various factors that the typical Mendelian mechanism is present in *Matthiola*. It cannot be argued here, as sometimes with *Oenothera*, that the genetic behavior of the genus or species is fundamentally non-Mendelian. Since the Mendelian mechanism is demonstrably present, and Muller's (1918) work on beaded wings in *Drosophila* seems to establish the adequacy of this mechanism in a closely parallel case, surely conventional factorial analysis should be carried as far as possible; in fact (Muller, 1918, p. 423), a Mendelian explanation should not be abandoned for anything short of positively contradictory evidence.

[25] Muller's (1918) complete report on the beaded-wing case in *Drosophila* appeared several months after the present paper had gone to the publisher. Certain conclusions given below, very similar to Muller's but not credited to him, were therefore reached independently.

In the *Drosophila* case just mentioned, the "principal" factor for the character in question is "dominant for its visible effect and recessive for a lethal effect," so that no pure beaded individuals appear among the progeny of beaded. The original race regularly gave progeny partly heterozygous beaded and partly homozygous normal, while after a long period of selection a true-breeding beaded race appeared. This latter form, it proved, fails to give normals not because of being duplex for beaded—it is still simplex—but because of its possession of another factor, known only by its lethal effect when homozygous, which is carried by the chromosome bearing the normal allelomorph of the factor for beaded. The locus of this recessive lethal factor gives in general about 10 per cent of crossovers with the locus of beaded, but in this case, because of the presence of a factor "which almost entirely prevents crossing over" between the loci of the two lethal factors, viable non-beaded zygotes are very rarely produced. Thus every zygote receiving either two beaded-carrying chromosomes or two non-beaded-carrying chromosomes of the pair concerned fails to develop, and all the insects produced are necessarily heterozygous for both lethal factors.

A point of special interest in this case is the fact that by certain crosses individuals can be produced which give certain types among their progeny in very small percentages. Muller suggests that part at least of the supposed mutants of *Oenothera* may be due to crossing over between chromosomes carrying lethal factors, by which certain recessive factors are permitted to come to expression in viable zygotes.

For the inheritance of doubleness of flowers in *Matthiola* he gives a "balanced-factor" explanation essentially identical with mine (Frost, 1915).

There seems to be little reason to doubt that the differential factors for these aberrant *Matthiola* types have originated by mutation. On the analogy of *Drosophila* we might expect that the true mutations would be relatively rare, and that most of the apparent mutants, in cases where they appear frequently, would be due to segregation, appearing as the result of crossing over in chromosomes carrying balanced lethal factors. The evidence seems to indicate, however, that the differential factors for the mutant types at all extensively studied are dominant for their visible effects and usually (probably imperfectly) recessive for a lethal effect, the mutant factors thus being genetically similar to the factor for beaded wings in *Drosophila*. This would seem to imply the occurrence of certain mutations in pro-

portions as high as about 1 per cent, and a general mutation coefficient of perhaps 4.5 per cent, while the only Mendelian alternative would seem to be some more complex scheme whose satisfactory formulation might require much more extensive hybridization data.

To be more specific: (1) these types are not single recessives, since they are not homozygous but split into the mutant and "normal" types; (2) they are not simple cases of multiple recessives, as has been proposed by Heribert-Nilsson (1915) for *Oenothera* mutations, since what is on that hypothesis the full dominant type reappears with selfing; (3) if these types are single dominants, as they appear to be, they cannot (barring the action of inhibiting factors) arise from the pure recessive "normal" or Snowflake type by segregation, but only by immediate mutation; (4) they are not simple cases of complementary dominant factors, since they occur among the progeny of selfed parents.

We might assume that a "mutant" type depends on two pairs of factors, one homozygous and the other heterozygous, while both pairs are heterozygous in the "mutating" Snowflake parent. Thus the crenate type might have the zygotic formula $\frac{D \quad Ci}{d \quad ci}$, where d is the factor for double flowers, C a dominant factor for crenate, and I a dominant inhibitor of C, all three loci being situated in the same chromosome, at distances of, say, 16 and 4 units apart, in the order indicated. A Snowflake parent producing crenate progeny would then be $\frac{DCI}{d\,c\,i}$ or $\frac{DCi}{d\,c\,I}$, and crossover combinations would produce the apparently mutant crenate progeny. The crenate progeny would behave as heterozygous dominants when selfed, and if CC zygotes were non-viable would yield constant Snowflake and inconstant crenate; the extracted Snowflake singles, having the composition $\frac{Dci}{dci}$, *could not throw crenate individuals* except by true mutation of c to C. With selfed Snowflake, if we assume 16 per cent and 4 per cent of crossing over in the two positions, and a 60-per-cent selective elimination of crenate zygotes, all CC zygotes being non-viable, substantially the observed percentages of crenate singles and doubles result.[26]

[26] See page 125, footnote. This scheme agrees fairly well with the results from crossing, and gives almost exactly the observed proportion of total doubles (a little over 53 per cent) for selfed Snowflake. Its adequate presentation must be reserved for a later paper.

Formerly (Frost, 1916) the hypothesis of frequent dominant mutations seemed the more probable, but there is apparently nonconformable evidence. It is true that the peculiar behavior of the slender type might conceivably depend on an occasional mutation in another locus, or an exchange (Shull, 1914) or duplication of loci, giving two similar or identical factors for slender. An apparently fatal objection, however, is the fact that the supposed mutants seem to show linkage with singleness or doubleness at their origin from Snowflake as well as in subsequent generations—a fact which strongly suggests segregation in the former case.

If the apparent mutants are really due to segregation complicated by lethal action, the origin of the complex heterozygosis indicated for Snowflake is doubtful; it may be due to hybridization, but more probably to a gradual accumulation of mutant factors in balanced-lethal combinations. On the analogy of Muller's *Drosophila* case, especially, it might be expected that the latter would be the true explanation, particularly since self fertilization seems to be the rule in *Matthiola*. On this basis the term *mutant type* is used with some confidence in this paper, while the aberrant individuals have been called *apparent mutants*.

We must not forget that some of the mutant types may arise, as with *Oenothera gigas* and *O. lata*, by non-disjunction, or reduplication of chromosomes, and that this fact may determine their heredity. This is not to be expected with the types whose factors show apparent coupling with singleness or doubleness, but it might be true of the apparently unlinked smooth-leaved type. A preliminary study of several types shows that the usual somatic number of chromosomes is probably fourteen, but that positive counts are difficult. While it might be very hard to demonstrate the regular presence of one extra chromosome in an individual or a type, it should be easy to decide between the diploid and triploid numbers. The large-leaved type is so strongly suggestive of *O. gigas* that it would not be surprising to find the triploid number in the material now on hand for examination.

In a preliminary paper on these types the writer (Frost, 1916) discussed some possible relations of mutation, heterozygosis, and partial sterility, with special reference to *Oenothera*, mentioning the possibility that special prevalence of heterozygosis in the genus may be, "in large part, a *result* rather than a *cause* of *mutation*." This suggestion is evidently justified even if much of the supposed mutation of *Oenothera* is really segregation, since it is highly probable that

the peculiar phenomena depend on lethal factors or combinations of factors originally due to mutation.

Another possibility there mentioned, advanced by Belling (1914) and since specially discussed by Goodspeed and Clausen (1917), is that of the occurrence of lethal *combinations* of certain factors which in other combinations may be in no way prejudicial to normal development. As the latter paper shows, it is probable that in certain crosses between "good species" most of the new combinations brought together in the formation of F_1 gametes are incompatible with the production of functional gametes. Perhaps in the case of *Oenothera* there may exist within a species factors lethal in any combination when homozygous, and other factors lethal only in certain combinations.

A balanced-factor explanation for the inheritance of doubleness[27] in *Matthiola*, a case which Muller (1918) discusses, seems to have been first definitely stated by Goldschmidt (1913), though he failed to provide for one feature of the evidence, the deviation of the heredity ratio from 50 per cent. As has been shown (Frost, 1915), this peculiarity may be due to greater viability of the homozygotes (sterile doubles) during embryonic development, since the doubles are more viable in the mature seeds and more vigorous in later development (Saunders, 1915). In this case the "normal" factor is completely eliminated in favor of the mutant (sterile-double) factor in the formation of the sperms, and probably is partially eliminated in the formation of either the eggs or the embryos or both.

Here the normal singleness (sporophyll) factor *D* may act as a lethal in the heterozygous parent, possibly from its general relations of growth vigor in the presence of the more vigorous *d*-carrying cells. If the lethal factor is situated in a distinct locus, evidently crossovers are at most extremely rare. It is true that Miss Saunders (1911) finds that F_1 hybrids with pure single forms produce functional single-carrying pollen; with the pure single forms from which the original "double-throwing" mutants arose, however, this might not be true, or a lethal change may have occurred in the singleness factor itself rather than in a factor coupled with it. The *Drosophila* case would suggest a lethal change in another locus of the single-carrying chromosome.

In my paper of 1915 this lethal change in one chromosome apparently accompanying the mutation of *D* to *d* in the homologous

[27] For a brief outline of the genetic behavior of doubleness see the discussion of the experimental data for the smooth-leaved type.

chromosome was considered puzzling. Evidently, however, it may have occurred in one chromosome before *D* mutated to *d* in the other, and even then may have produced its lethal effect. It is evident that if doubleness should arise in the absence of the lethal effect it would tend to be eliminated by the return of one-third of the singles to the homozygous condition in each generation. In fact, it is possible that the lethal change arose later than doubleness, as in the *Drosophila* case, or was brought in later by cross pollination, and happened to be preserved as a result of horticultural selection for a high proportion of doubles.

A parallel-column comparison between the double type and the types especially discussed above has already been given, in connection with the smooth-leaved type. It will now be seen that this comparison seems to apply to all mutant types, except early, that have been genetically tested, the principal differences between these types relating to the heredity percentage and the apparent presence or absence of linkage with the single-double factors.

From the standpoint of its relation to genetic analysis the doubleness factor is remarkably similar to the sex factor in animals. There are two types in each generation, one heterozygous and the other evidently homozygous, and these types are produced by the fertilization of two kinds of eggs, produced in equal or nearly equal numbers, by a single kind of sperm. Although one of the somatic types is sterile, and the uniformity of the sperms produced by the other is due (evidently) to lethal action, the opportunity for chromosome analysis is similar to that with sex chromosomes.

We may say that the doubleness factor and its normal allelomorph (*d* and *D*) are carried by chromosome pair I. Already we know several other pairs of factors evidently carried by this pair of chromosomes. These are, to name only the mutant or possibly mutant member of each pair of factors: *P* (pale sap color) and *W* (colorless plastids), both studied by Miss Saunders (1911, 1911*a*); *C* (crenate-leaved), *S* (slender; possibly two factors), and *N* (narrow-leaved). As we have seen, the last three of these are probably lethal when homozygous, and one or more unidentified lethal factors may be concerned in the breeding results, while the doubleness factor affects the race much like a recessive lethal, since all *dd* individuals are completely sterile.

SUMMARY

This paper describes the occurrence, characteristics, and heredity of certain aberrant plant types which decidedly resemble some of the "mutant" types produced by *Oenothera lamarckiana*. The parent form is *Matthiola annua* Sweet, of the horticultural variety "Snowflake."

These aberrant forms may be called mutant types, since it is highly probable that they are originally produced by mutation. The aberrant individuals may be termed apparent mutants, since it may be considered uncertain whether they usually arise by immediate mutation or by segregation. The case acquires special significance because individuals belonging to the mutant types, although the species is known to be typically Mendelian with respect to various characters, give erratic heredity ratios suggestive of *Oenothera*.

At least eight types have been somewhat carefully studied, and six of these have shown their heritability in progeny tests. Several other types have been named, but for various reasons their distinctness is more or less doubtful.

Some of the commoner types have each been produced by many parents, and in several pure lines isolated from the original commercial variety. The apparent mutants other than the early type compose about four or five per cent of the progeny of Snowflake and early parents, the separate types ranging down from about one per cent.

Most of the mutant types are in general inferior to Snowflake in vigor, and the difference in development is greatly increased by certain unfavorable environmental conditions. The proportion of apparent mutants in cultures from Snowflake parents appears to be definitely lower where germination is comparatively poor.

The mutant types differ from Snowflake and from each other in various respects. The early type is practically a smaller and earlier Snowflake. The other mutant types, on the other hand, differ markedly from Snowflake in vigor, fertility, and various form and size characters. Each type is named from some conspicuous characteristic difference from Snowflake, but usually various other differences can readily be found.

Somewhat extensive progeny tests have been made for five of the mutant types, and a little evidence secured for two or three other types.

The early type is probably due to a single dominant mutant factor segregating normally from the corresponding Snowflake factor; the quantitative nature of its differences from Snowflake, however, makes positive determination of this point a matter of great difficulty.

At least five other types plainly reproduce themselves, but about 50 to 70 per cent of the progeny are usually Snowflake; no true-breeding individual of any generation of any of these types has yet been tested. Genetic work with most of these types has been much hampered or even prevented by low vigor and fecundity, and the aggregate data from progeny of parents of four types strongly indicate selective viability at germination. It has been determined by crossing that in three of the types the mutant factor (or factors) is carried both by eggs and by sperms. From these facts it seems probable that homozygotes of the mutant types are non-viable, and that severe selective elimination occurs during embryonic development; or, in other words, that the mutant factor is imperfectly recessive for a lethal effect.

In three types there appears to be linkage with the factor pair for singleness and doubleness of flowers, the mutant factor being coupled with singleness in the tested apparent mutants of two types, and with doubleness in the third type. With two other types these factors seem to be independent. No reversal of coupling has been found in later generations of the former two types, but on the scheme presented crossover singles should be scarce.

For one type (crenate-leaved) a hypothesis based on the facts stated gives very closely the ratio obtained from selfed parents. Reciprocal crosses with Snowflake conform less closely to the requirements of the hypothesis, but do not definitely contradict it. The slender type, which shows similar apparent linkage, seems to disagree definitely with the hypothesis; there is strong evidence, however, that slender individuals may differ genetically among themselves.

A more complex scheme providing also for the usual origin of these types from Snowflake by segregation is briefly outlined.

The selfing ratios are very suggestive of duplication of a chromosome (non-disjunction), as in *Oenothera lata*, but it is hard to reconcile the cases of apparent linkage with this hypothesis. It seems probable that these three linked types have originated and are transmitted in the same general way as the double-flowered type, and that all of these four mutant factors (including double) represent changes of some sort within a chromosome of the same pair, which may be

numbered I. Miss Saunder's work shows that two flower-color factors also belong to this linked group.

The large-leaved type strikingly resembles *Oenothera gigas*, and it may prove to be triploid in nuclear constitution. In that case segregation may be irregular and genotypically intermediate individuals may be more or less frequently produced.

It is probable that further study of these types will help to explain the remarkable genetic behavior of *Oenothera* and of *Citrus*.

LITERATURE CITED*

Atkinson, George F.

1917. Quadruple hybrids in the F_1 generation from *Oenothera nutans* and *Oenothera pycnocarpa*, with F_2 generations and back- and intercrosses. Genetics, vol. 2, pp. 213–260, 11 tables, 1 diagr., 15 figs.

Babcock, Ernest B.

1918. The rôle of factor mutations in evolution. Am. Naturalist, vol. 52, pp. 116–128.

Bartlett, H. H.

1917. Mutation in *Matthiola annua*, a "Mendelizing" species. [A review of paper of same title by H. B. Frost.] Bot. Gaz., vol. 63, pp. 82–83.

Bateson, William, and Saunders, Edith R.

1902. Experimental studies in the physiology of heredity. I. Experiments with plants. *Matthiola*. III. Discussion. Roy. Soc. London, Reports to the Evolution Committee, vol. 1, pp. 32–87, 125–160, 15 tables.

Bateson William, Saunders, Edith R., and Punnett, Reginald C.

1905. Experimental studies in the physiology of heredity. *Matthiola*. Roy. Soc. London, Reports to the Evolution Committee, vol. 2, pp. 5–44, tables.

1906. *Ibid.* Stocks. *Ibid.*, vol. 3, pp. 38–53, 4 tables, 2 figs.

Bateson, William, Saunders, Edith R., Punnett, Reginald C., and Killby (Miss) H. B.

1908. Experimental studies in the physiology of heredity. Stocks. Roy. Soc. London, Reports to the Evolution Committee, vol. 4, pp. 35–40, 3 tables.

Belling, John.

1914. The mode of inheritance of semi-sterility in the offspring of certain hybrid plants. Zeitschr. f. indukt. Abstam.- u. Vererbungsl., vol. 12, pp. 303–342, tables, 17 figs.

Blakeslee, Albert F., and Avery, B. T. Jr.

1919. Mutations in the jimson weed. Jour. Heredity, vol. 10, pp. 111–120, 11 figs.

* An asterisk prefixed to the date indicates that the paper cited has not been seen by the present writer.

Correns, Carl E.

1900. Über Levkojenbastarde. Zur Kenntniss der Grenzen der Mendel'schen Regeln. Bot. Centralbl., vol. 84, pp. 97–113.

1902. Scheinbare Ausnahme von der Mendel'schen Spaltungsregel für Bastarde. Deutsch. bot. Ges., Ber., vol. 20, pp. 159–172, 4 tables.

Davis, Bradley, M.

1917. A criticism of the evidence for the mutation theory of de Vries from the behavior of species of *Oenothera* in crosses and in selfed lines. Nat. Acad. Sci., Proc., vol. 3, pp. 705–710.

Frost, Howard B.

1911. Variation as related to the temperature environment. Am. Breeders' Assoc., Ann. Rept., vol. 6, pp. 384–395, 4 tables, 4 charts.

1912. The origin of an early variety of *Matthiola* by mutation. *Ibid.*, vol. 8, pp. 536–545, 5 tables.

1915. The inheritance of doubleness in *Matthiola* and *Petunia*. I. The hypotheses. Am. Naturalist, vol. 49, pp. 623–636, 1 fig., 2 diagr.

1916. Mutation in *Matthiola annua*, a "Mendelizing" species. Am. Jour. Bot., vol. 7, pp. 377–383, 3 figs.

1917. A method of numbering plants in pedigree cultures. Am. Naturalist, vol. 51, pp. 429–437.

Gates, R. Ruggles.

1915. The mutation factor in evolution. London, Macmillan, xiv + 353 pp., 1 map, 114 figs., bibl.

Goldschmidt, Richard.

1913. Der Vererbungsmodus der gefüllten Levkojenrassen als Fall geschlechtsbegrenzter Vererbung? Zeitschr. f. indukt. Abstam.- u. Vererbungsl., vol. 10, pp. 74–98, diagr.

1916. Nochmals über die Merogonie der Oenotherabastarde. Genetics, vol. 1, pp. 348–353, 1 pl.

Goodspeed, Thomas H., and Clausen, R. E.

1917. Mendelian-factor differences *versus* reaction-system contrasts in heredity. Am. Naturalist, vol. 51, pp. 31–46, 92–101.

Heribert-Nilsson, N.

*1915. Die Spaltungserscheinungen der *Oenothera lamarckiana*. Lunds Univ. Årsskrift, vol. 12, pp. 4–131. (Review by Ben C. Helmick *in* Bot. Gaz., vol. 63, 1917, pp. 81–82.)

Muller, Hermann J.

1917. An *Oenothera*-like case in *Drosophila*. Nat. Acad. Sci., Proc., vol. 3, pp. 619–626.

1918. Genetic variability, twin hybrids and constant hybrids, in a case of balanced lethal factors. Genetics, vol. 3, pp. 422–499, 1 table, 1 fig., 1 diagr.

Saunders, Edith R.

1911. Further experiments on the inheritance of doubleness and other characters in stocks. Jour. Genetics, vol. 1, pp. 303–376, 8 tables.

1911*a*. The breeding of double flowers. Fourth Intern. Conf. on Genetics, Proc., pp. 397–405, diagr.

*1913. Double flowers. Roy. Hort. Soc., Jour., vol. 38, pt. 3, pp. 469–482.

1913*a*. On the mode of inheritance of certain characters in double-throwing stocks. A reply. Zeitschr. f. indukt. Abstam.- u. Vererbungsl., vol. 10, pp. 297–310.

1915. A suggested explanation of the abnormally high records of doubles quoted by growers of stocks (*Matthiola*). Jour. Genetics, vol. 5, pp. 137–143, 3 tables.

1916. On selective partial sterility as an explanation of the behavior of the double-throwing stock and the petunia. Am. Naturalist, vol. 50, pp. 486–498.

SHULL, GEORGE H.

1914. Duplicate genes for capsule form in *Bursa bursa-pastoris*. Zeitschr. f. indukt. Abstam.- u. Vererbungsl., vol. 12, pp. 97–149, 5 tables, 7 figs.

"STUDENT."

1908. The probable error of a mean. Biometrika, vol. 6, pp. 1–25, tables, 4 diagr.

1917. Tables for estimating the probability that the mean of a unique series of observations lies between $-\infty$ and any given distance of the mean of the population from which the sample is drawn. *Ibid.*, vol. 11, pp. 414–417, tables.

SWINGLE, WALTER T.

1911. Variation in first-generation hybrids (imperfect dominance): its possible explanation through zygotaxis. Fourth Intern. Conf. on Genetics, Proc., pp. 381–393, 10 figs.

TSCHERMAK, ERICH VON.

*1904. Weitere Kreuzungsstudien an Erbsen, Levkojen u. Bohnen. Zeitschr. f. d. landw. Versuchswesen in Oesterreich, 1904, pp. 533–638.

1912. Bastardierungsversuche an Erbsen, Levkojen, und Bohnen mit Rücksicht auf die Faktorenlehre. Zeitschr. f. indukt. Abstam.- u. Vererbungsl., vol. 7, pp. 81–234, tables.

WEBBER, HERBERT J.

1906. Pedigree records used in the plant-breeding work of the Department of Agriculture, *in* L. H. Bailey, Plant Breeding (New York, Macmillan), pp. 308–319.

DE VRIES, HUGO.

1906. Species and varieties: their origin by mutation. Ed. 2, Chicago, Open Court Pub. Co., xviii + 847 pages.

1918. Twin hybrids of *Oenothera hookeri* T. and G. Genetics, vol. 3, pp. 397–421, 14 tables.

1919. *Oenothera rubrinervis*, a half mutant. Bot. Gaz., vol. 67, pp. 1–26, tables.

YULE, G. UDNY.

1911. An introduction to the theory of statistics. London, Charles Griffin & Co., xiii + 376 pages, 53 figs.

PLATE 22

The Early Type

Fig. 1. March 20, 1908. The single progeny of WG9. Plants from house M to the reader's left from stake, from house W to right of stake, from house C below. WG9–C10, the early apparent mutant, is the middle plant in the lower row. The stake indicates inches.

Fig. 2. About May 1, 1908. WG9–C10 at the left, WG9–C9 (Snowflake) at the right.

Fig. 1

Fig. 2

PLATE 23

The Early Type

Fig. 3. April 8, 1909. The single progeny of WG9–C9 (Snowflake); arrangement as in figure 1.

Fig. 4. April 9, 1909. The single progeny of WG9–C10 (heterozygous early). Warm-house plants partly at right of stake in lower row; arrangement otherwise as in figure 3. Compare with figure 3, house by house.

Fig. 3

Fig. 4

PLATE 24

The Early Type

Fig. 5. July 19, 1911. Lots 1 to 10, with lots 11 to 14 mostly in sight at the right. Odd-numbered lot in nearer (west) half of each row.

Fig. 6. July 19, 1911. Lots 19 to 28, with lots 15 to 18 mostly in sight at the left.

Fig. 5

Fig. 6

PLATE 25

The Smooth-leaved Type

Fig. 7. April 27, 1909. Smooth-leaved apparent mutants. Compare with figures 3 and 4 as to earliness, noting the difference in date.

Fig. 8. May 29, 1914. Progeny of a smooth-leaved parent. Plant at right Snowflake single, the others smooth.

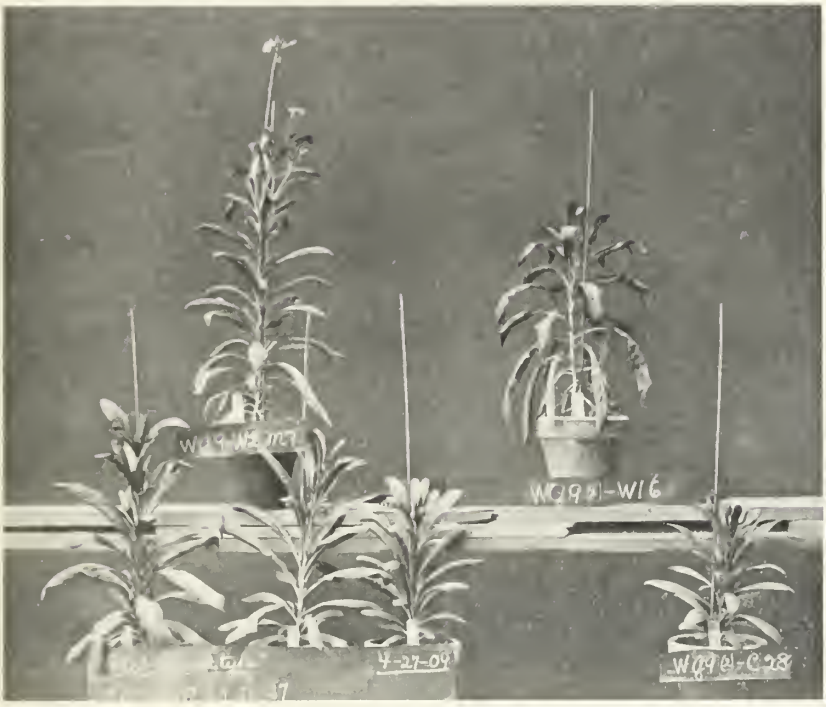
WQ99-W16
4-27-09
WQ99-C28

Fig. 7

SMOOTH-
LEAVED
SMOOTH-
LEAVED
SNOWFLAKE

Fig. 8

PLATE 26

THE SMOOTH-LEAVED TYPE

Fig. 9. June 28, 1915. Progeny of a smooth-leaved parent. Smooth single at left, Snowflake double at right.

Fig. 10. Same date and parent as with figure 9. From left to right: Snowflake double (also shown in figure 9), Snowflake single, smooth double.

Fig. 9

Fig. 10

PLATE 27

The Large-leaved Type

Fig. 11. August 29, 1914. Progeny of a large-leaved parent (28a), near the close of the hot Riverside summer. From left to right: large single, large double, Snowflake single (two, the first injured by aphids).

Fig. 11

PLATE 28

The Large-leaved Type

Fig. 12. July 8, 1916. Progeny of a large-leaved parent. Middle plant Snowflake; the rest large; all single.

Fig. 13. July 8, 1916. Progeny of a large-leaved parent, more than a month older than those shown in figure 12. From left to right: large double, Snowflake double, large single.

Fig. 12

Fig. 13

PLATE 29

The Crenate-leaved Type

Fig. 14. April 6, 1909. Crenate-leaved apparent mutants. Note the variation in leaf serration, and especially the slightness of the serration (or crenation) with the one cool-house plant (below).

Fig. 15. April 14, 1911. Progeny of a crenate-leaved parent, grown in a cool greenhouse. The first two plants at the right are Snowflake, the rest crenate.

House W
House W
WG4
-C16
-C10

Fig. 14

PARENT
P. = WG4 -W1-W2
Normal
No 8
No 9
No 12
No 13
No 15
No 10
No 14

Fig. 15

PLATE 30

The Crenate-leaved Type

Fig. 16. July 8, 1916. Progeny of a crenate-leaved parent. From left to right: crenate single (two), crenate double, Snowflake double.

Fig. 17. July 8, 1916. Snowflake × crenate-leaved, F_1. From left to right: smooth, Snowflake single, crenate double (two).

Fig. 16

Fig. 17

PLATE 31

The Slender Type

Fig. 18. April 27, 1909. Miscellaneous aberrant individuals, with two typical Snowflake plants (third from the left above, second from the left below). In upper row: second from left, narrow double; second from right, slender double. In lower row at left, slender single (25b).

Fig. 19. April 14, 1911. Progeny of a slender parent (25b). Two at the right Snowflake, the rest slender.

Fig. 18

Fig. 19

PLATE 32

The Slender Type

Fig. 20. June 3, 1914. Progeny of slender parents. From left to right: slender single, slender double, Snowflake double.

Fig. 21. July 7, 1916. Snowflake × slender, F_1. Middle plant Snowflake; the others slender; all single.

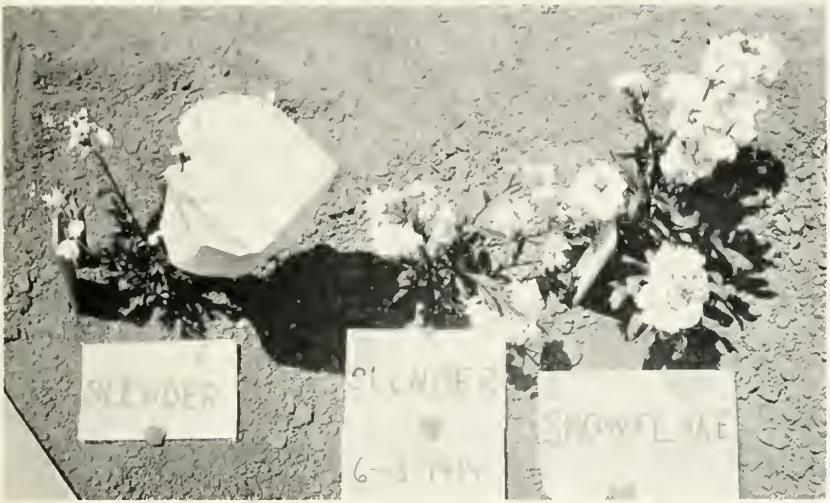

Fig. 20

Fig. 21

PLATE 33

The Narrow-leaved Type

Fig. 22. April 13, 1911. Narrow-leaved apparent mutants.

Fig. 23. June 3, 1914. A narrow-leaved apparent mutant among progeny of a crenate-leaved parent. From left to right: narrow double, crenate single (two).

P1=WG9
4-13-11
P1=WS1
P1=WG9
-C10-C2
sym3-M11
(2)-W16
(2)-W25
sym3-M10-C10-W6

Fig. 22

Fig. 23

PLATE 34

THE NARROW-LEAVED AND SMALL-SMOOTH-LEAVED TYPES

Fig. 24. June 28, 1915. A narrow-leaved apparent mutant among F_1 progeny from Snowflake × slender. Narrow double at left; the rest Snowflake single.

Fig. 25. April 14, 1911. Miscellaneous aberrant plants, some being apparent mutants. From the left: first and fifth small-smooth, third stout dwarf, seventh slender. See text.

Fig. 24

Fig. 25

PLATE 35

The Narrow-dark-leaved Type

Fig. 26. June 3, 1914. A narrow-dark-leaved apparent mutant among progeny of a narrow-leaved parent. Third plant from left narrow-dark single; the other three Snowflake double.

Fig. 27. June 28, 1915. Progeny of a "small-convex-leaved(?)" parent (27a). From left to right: narrow-dark single, Snowflake double, smooth single.

Fig. 26

Fig. 27